Natural and Sexual Selection in Three Species of Odonates

by

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ABSTRACT

Evolution is driven mainly by natural and sexual selection, which can be confounded by sex, mating system and environmental influences. Odonates have three important selective episodes during the adult life stage: survival to sexual maturity; survival after sexual maturity and mating success. Using mark-recapture and logistic regression, I examined natural selection in adult males and females of two species of non-territorial damselflies, *Lestes congener* and *Lestes disjunctus* (Odonata: Zygoptera) and one species of territorial dragonfly, *Sympetrum pallipes* (Odonata: Anisoptera) in two successive years at Galiano Island, B.C. Females gained more mass over the maturation period than males, but the difference was smaller in territorial *S. pallipes*. Sexual size dimorphism was therefore greater at maturity than emergence but less so in *S. pallipes*. Female survival was lower than male survival over the maturation period and survival over the maturation period was lower than survival after maturity in some groups. Before maturity, small male *L. congener* survived better and male *S. pallipes* with small wing loading values survived less well. No measurable difference was found between female and male survival after maturity in any species and wing loading was a better predictor of survival than body size. I also tested for sexual selection on males of all three species. As predicted, selection on body size was not detectable in both *Lestes* species. In male *S. pallipes*, small males had a mating advantage early in the season but large males had an advantage late in the season. This was attributed to density or weather effects. Large male *S. pallipes* had greater territorial success, but were not more likely to achieve mating success. There were large differences in body size between years in all groups, but the direction of change did not correspond with the direction of selection. The importance of measuring selection over more than one generation and improved observational methods are discussed further.

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General Introduction

Evolution determines the trajectory of the genotype distribution of a population, in large part through selection on a trait or series of traits and the heritability of those traits. Selection is defined as the covariance between reproductive success and trait values (Endler 1986). To differentiate between selection that arises from mating success and that which arises from survival, or longevity, Darwin (1859; 1871) proposed that evolution is governed by both sexual (mating success) and natural (survival) selection. Phenotype is the physical expression of genotype, but phenotype is also affected by environment and ecological circumstance, including foraging success, predation and competition. Selection acts on phenotype rather than genotype, and the strength and direction of selection along with the degree to which phenotype is heritable determines evolution. Body size is an obvious phenotypic expression of genotype and is thought to play a role in mating success and survival in many species. In flying insects, body size can determine maneuverability, and thus the ability to not only catch prey on the wing, but also to avoid predators (e.g., Marden 1988; 1994). Further, many insect species mate on the wing and body size is thought to be an important component of the ability of males to acquire matings and engage in male-male mating competition (e.g., Anholt 1991; Fincke 1982; Grether 1996b; Koenig and Albano 1987; McVey 1988; Michiels and Dhondt 1991; Sokolovska et al. 2000).

Evolutionary success is measured as the lifetime reproductive success (LRS) of an individual, but this can be difficult or impossible to measure in the field. To facilitate an understanding of the relative nature and importance of natural and sexual selection pressures, LRS can be broken down into separate identifiable episodes in the life history of an organism. Mating success is the *sine qua non* of reproductive success and is often measured as the number of matings achieved by an individual. Mating, however, presupposes survival. In many plants and animals, survival before maturity is qualitatively different than after maturity, with a different suite of demands that determine fitness. In mayflies (Ephemeroptera), for example, sexually mature adults lack usable mouthparts because the singular purpose of individuals is to mate (Borror et al. 1989). In adult damselflies (Odonata: Suborder Zygoptera) and dragonflies (Odonata: Suborder Anisoptera), the brief period prior to maturity is characterized by active foraging associated with rapid mass gain followed by a period of intense competition for matings after sexual maturity (Corbet 1999). Thus, at least three important selective episodes can be identified in adult odonates: mating success, survival to maturity and survival after maturity.

Odonata, including Suborders Anisoptera (dragonflies) and Zygoptera (damselflies), displays a large variation in mating behaviour, even among morphologically similar species (Corbet 1999), and are therefore useful for the study of the relationship between mating behaviour and selection. Odonates are useful for natural selection studies because: 1) they tend to gather around small water bodies such as ponds for much of their adult life; 2) they can be observed throughout their short adult lifespan of 5-8 weeks (Corbet 1999), making estimates of adult survival and reproductive success possible; 3) they are large and therefore easy to mark and observe; 4) different species with distinct behavioral systems can be observed within the same habitat. Due to these characteristics, odonates have been the subject of several studies of natural and sexual selection (e.g., Anholt 1991; Cordero 1995; Fincke 1986; Grether 1996b; Harvey and Walsh 1993; Kasuya et al. 1997a; Koenig and Albano 1987; McVey 1988; Michiels and Dhondt 1991; Moore 1990; Stoks 2000).

Biology of odonates

Odonates are typically univoltine, primarily diurnal insects. Larvae are almost always aquatic. Emergence takes place in the spring and summer in temperate zone species when mature larvae climb out of the water. After eclosion, exoskeletons are soft and wings are wet and adults are temporarily unable to fly for a period of one to two hours (Corbet 1999). Known as tenerals during this stage, odonates are defenseless and exposed to predation risks. After the exoskeleton hardens, odonates leave the place of emergence and go through a period of sexual maturation, which takes one to two weeks (Corbet 1999). During this time, there is a period of rapid mass gain necessary for reproduction, although exoskeleton size is fixed at emergence. Female odonates do not have a full complement of eggs at emergence (Pajunen 1962) and tend to increase their mass by a factor of 1.2 to 3.5 between emergence and sexual maturity, while males increase their mass by a factor of 0.85 to 3.2, although mass gain is typically much larger in territorial than non-territorial species (Anholt et al. 1991).

After reaching sexual maturity, odonates return to the emergence site, although some emigration to other water bodies does occur (i.e., Anholt 1990b; Thompson 1991). The emergence site thus becomes the rendezvous site where individuals attempt to mate and oviposit. Operational sex ratios at the rendezvous site are typically highly male-biased (Corbet 1999). Thus, while most females mate, competition among males for matings is intense.

Males spend much of their time at the rendezvous site awaiting opportunities for mating attempts. Male-male competition takes various forms ranging from scramble competition to resource-defense polygyny, or territoriality, in which males compete to hold the highest-quality territory. In scramble competition, males gather at sites where encounters with females are likely and attempt to couple with them. Successful pair forming in these is thought to be mainly due to chance, although males can increase their chance of encounters with females by staying at the rendezvous site as long as possible.

In territorial systems, males establish territories in suitable oviposition sites and actively defend them against conspecific males. Rival males assess each other and disputes are thought to be typically resolved in favor of the resident (Waage 1988). Escalated disputes occur when competitors aggressively attack and chase each other but they are avoided when possible because they are energetically expensive (Marden and Waage 1990). They are more likely to occur when there is uncertainty in the resident-intruder asymmetry (Waage 1983, 1988), for example when both individuals perceive they have resident status. Resident / satellite (those males not currently holding a territory) roles can change and may depend on current energy reserves (Plaistow and Siva-Jothy 1996). Resident males of some species tolerate subordinate males within their territories (Koenig and Albano 1985), but others do not (Campanella and Wolf 1974). Odonates appear to be sensitive to some environmental cue or suite of cues because males hold territories that have a high hatchability rate, and females may choose territories preferentially, rather than choosing a specific territory holder (eg., Koenig 1991; Tsubaki et al. 1994).

High fat content is often correlated with mating success in territorial males (e.g., *Calopteryx maculata,* Maarden and Waage, 1990; Maarden and Rollins 1994; *C. splendens xanthostoma*, Plaistow and Siva-Jothy, 1996). In male *C. maculata*, for example, winners were fatter in 68% of short contests and 95% of long contests, and the duration of disputes was positively correlated with average fat content of contestants (Marden and Waage 1990). However, territoriality is energetically costly: territorial male *Pachydiplax longipennis* spent about 85% of their total available energy in defense of their territories (Fried and May 1983), and Corbet (1980) found that escalated disputes that displace residents cost both participants 40-50% of their energy reserves. Territorial males have few chances to rejuvenate energy stores because they rarely forage while defending territories (Fried and May 1983).

Territorial dominance is not temporally fixed. Since energy costs of territory defense are high, individuals probably only have enough energy to defend their territories for a limited amount of time each day (Campanella and Wolf 1974). There is also often likely a temporally restricted daily optimum for high female density and receptivity of copulation attempts (Campanella and Wolf 1974). Campanella (1975) identified two strategies for optimizing territorial activities: time-optimization (*Plathemis lydia*), where there is a daily optimal time for mating; and energy-optimization (*Libellula quadrimaculata*), where there is no daily optimum.

Regardless of mating system, when a sexually mature male encounters a female, he attempts to grasp her from above by the prothorax (Zygoptera) or the head (Anisoptera) and thus form a tandem position with her. The male will then invite the female to copulate, perhaps by flexing his abdomen, to which the female may or may not comply. If the female complies, the male will then transfer sperm from his primary genitalia located on the ninth abdominal segment, and transfer it to the secondary genitalia located on the second or third abdominal sternite. This arrangement is unique among insects (Corbet 1999). A male can refuse to let go of a female, but he cannot force her to mate with him because the female must raise her abdomen to meet his secondary genitalia in order for the male to make the sperm transfer (Fincke 1997). A female can refuse to mate and can try to refuse a copulation attempt but this can be energetically expensive and sometimes fatal (Fincke 1997; Koenig 1991). However, mating unnecessarily can also be energetically expensive; this is evidenced by the fact that females often attempt to refuse mates (e.g., Koenig 1991; Ruppell 1989). The female therefore has to make a cost-benefit decision when confronted with the possibility of unnecessarily remating.

Also unique to odonates, with very few exceptions in those species studied, is sperm removal (e.g., Waage 1979; Waage 1984b, 1986). In almost all zygopterans and most anisopterans, males have specially adapted penises that can remove, dislodge, displace or dilute the sperm of a female's previous mates during copulation. This leads to high rates of sperm precedence in which the last male to mate with a female is likely to successfully inseminate the majority of her eggs, assuming she does not remate prior to oviposition (e.g., Cordero and Miller 1992; McVey and Smittle 1984; Michiels and Dhondt 1988; Sawada 1998; Siva-Jothy and Tsubaki 1994).

Copulation can take a few seconds to several hours. Post-copulatory mate-guarding by males is common. Benefits of guarding to male fitness are threefold: it prevents takeover of the female by rival males; it induces the female to lay all or most of her current batch of eggs at a specific site, usually at or near the male's territory in territorial species; and it induces the female to oviposit as many eggs as rapidly as possible (Corbet 1999). Guarding also has several effects on the fitness of females: they are more likely to oviposit directly after copulation and oviposit for a longer duration; they are less susceptible to predation and drowning; they are less likely to remate during or after oviposition; they are less likely to accept copulation from rival males, and have reduced energy expenditures during oviposition (Corbet 1999). All these results, except the last, directly benefit male fitness and therefore encourage mate-guarding.

Mate-guarding is thought to have evolved as a response to sperm removal because a male can only be sure he is inseminating the eggs if the female oviposits before remating. It may take one of two forms: contact or non-contact. Contact mate guarding, in which the male remains in tandem with the female after mating, is primarily found in species in which males scramble for mates. These males have little opportunity to remate due to typically male-biased operational sex ratios, and therefore benefit more from ensuring their mate oviposits the eggs inseminated by them rather than by searching for more mates. Many territorial species have evolved non-contact mate guarding in which males attempt to prevent other males from copulating with their mates after copulation but before or during oviposition. This evolved because a small number of territorial males control necessary resources (the oviposition site) to which females need access. As a result, a territorial male may have numerous copulation opportunities and he often benefits more by attempting to copulate with other females than by contact guarding his previous mate.

Classification of odonate mating systems

Odonate mating systems have been reviewed by Campanella (1975), Waage (1984b), Conrad and Pritchard (1992), Fincke (1997) and Corbet (1999). Most classification systems draw heavily on ideas proposed by Emlen and Oring (1977) in their work on the mating behavior of birds, which proposes that classification systems should be divided into two main groups: *resource-based* systems and *non-resource-based* systems. They proposed that the distribution and abundance of either resources (in this case oviposition sites) or females or both determine the degree and type of competition that is profitable for males. Theoretically, as resources become too extensive or widely dispersed for an individual male to monopolize, or as females become more synchronous in their receptivity, searching for mates becomes more profitable for males than localized defense of encounter or oviposition sites and *vice versa* (Fincke 1997). Integral to most mating systems is the degree to which males control female access to the oviposition site. Conrad and Pritchard (1992) further divided Emlen and Oring's groups into five separate systems based on the frequency of intersexual encounters, the ability of males to monopolize resources necessary for reproduction and the predictability of female occurrence. Corbet (1999) proposed a further refinement of classification into six systems that differs from others by placing more emphasis on the phenomenon of sperm precedence, which he argues has been a dominating selective force on odonate mating systems, and further divides territorial species into two groups depending on the duration of copulation.

Biology of Lestes *and* Sympetrum

Lestes congener and *L. disjunctus* both belong to the Lestidae (Suborder Zygoptera), a small family commonly known as spreadwing damselflies (Cannings 2002). Like most zygopterans, they are non-territorial (Bick and Bick 1961; Bick and Hornhuff 1965; Corbet 1980), displaying typical scramble competition for mates (pers. obs.). Males at my study site typically displayed contact mate guarding. According to Conrad and Pritchard's classification system, both *L. congener* and *L. disjunctus* should fall into the resource limitation system because male-female encounters are not rare, males are not able to control resources and the occurrence of females is predictable.

The genus *Sympetrum* belongs to the Libellulidae (Suborder Anisoptera), a large family of dragonflies, commonly known as skimmers, with worldwide distribution. In contrast to *Lestes, Sympetrum* are considered territorial, with some variation in intensity of territoriality among species (Michiels and Dhondt 1991; Ueda 1979; Van Buskirk 1986, 1987). Personal observation has confirmed that *S. pallipes* males establish territories suitable for oviposition to attract females and actively defend them from conspecific males. In this study, *S. pallipes* males displayed both contact and non-contact mate guarding and females were rarely observed ovipositing without a male present.

Natural selection

Natural selection is differential survival relative to a measured trait. In odonates, there are four distinct life stages that an individual must survive to reproduce: the egg stage, the larval stage, pre-maturity and post-maturity. Growth is critical for development in the first two stages; this requires active foraging that may put an individual at greater risk of predation (Kohler and McPeek 1989; Stoks and Johansson 2000; Werner and Anholt 1993; Werner and Gilliam 1984). This suggests that there is a fundamental trade-off between growth and survival. If this is true, then survival should be lowest during those stages in which growth is the largest. Correspondingly, if mortality is higher, the opportunity for selection should also be higher. Further, within a given life stage, those individuals with the greatest growth should also experience greater mortality and thus have higher potential for selection.

The odonate larval stage varies greatly in length. In some smaller species, such as *L. disjunctus* (Duffy 1994), in which larvae hatch in the spring and emerge in the summer, it may last only a few months. Larger species can remain as larvae for up to five years (Corbet 1999). Overall survivorship through the larval stage is rarely greater than 10% (e.g., Anholt 1994; Benke and Benke 1975; Duffy 1994; Johnson 1986; Lawton 1970; Wissinger 1988) due to predation, cannibalism and intense competition. The opportunity for selection is thus very high during the larval stage, but survival in the wild is very difficult to detect and beyond the scope of this study.

The second discrete life stage begins at emergence. As noted above, tenerals are initially exposed to high predation risk. Following dispersal from the emergence site, odonates undergo a period of rapid mass gain to gather resources necessary for reproduction. This rapid mass gain necessitates active foraging that puts odonates at a continued risk of predation.

While few studies have demonstrated a difference in survival before and after maturity, fewer have separated recapture rates from survival. Thus, recapture is confounded with survival and estimates are likely inaccurate. In *Lestes temporalis*, both males and females had lower daily survival at the beginning and end of the season (male survival: day 1-5, 0.966; day 6-60, 0.996; day 61-80, 0.989; day 81-100, 0.936. female survival: day 1-5, 0.933; day 6-60, 0.996; day 61-80, 0.972; day 81-100, 0.925), but the authors attributed the difference in survival immediately after emergence to a marking effect (Ueda and Iwasaki 1982). This species, however, has a very long maturation period of about 90 days, during which time individuals estivate and predation risk is thus much lower than during times of activity. A similar post-release decline was detected in male *Mnais pruinosa*, after which daily survival was relatively constant at about 0.944 for both sexes before dropping off steeply at about 60 days, but the authors again attributed the decline to a marking effect (Nomakuchi et al. 1988). Post-emergent *Argia chelata* had lower survival in the first day following emergence, but the authors attributed the difference to emigration (Hamilton and Montgomerie 1989). Teneral *Pyrhossoma nymphula* had survival rates that were not different from, and possibly higher than, mature adults (Bennett and Mill 1995). In contrast, survival in male and female *Ischnura elegans* was found to be lowest at the beginning and end of the adult lifespan and higher in the interim (Parr and Parr 1972). Unfortunately, since the survival rates in all these studies may have been confounded by recapture estimates, it is not known if these estimates are accurate.

Over the maturation period, females gain more mass than males, but the difference is greater in non-territorial than territorial species (Anholt et al. 1991). In both sexes, mass gain consists of flight muscle tissue and fat reserves (Marden and Waage 1990), but males gain mostly thoracic mass while females gain abdominal mass, including egg clutches (Anholt et al. 1991; Marden 1989a). Mass gain comes at the expense of predator avoidance because animals must be active to forage; if this increases predation risk, survival should be lower in groups that gain relatively more mass. Thus, survival should be lower in females than males over the maturation period and the opportunity for selection should be higher.

Females have been found to have lower relative survival than males over the period of sexual maturation in at least four damselflies (Anholt 1991; Bick and Bick 1961; Garrison 1978; Hamilton and Montgomerie 1989) and one libellulid dragonfly (Koenig and Albano 1987). Female *Enallagma hageni* were recaptured in lower proportions than males after release at emergence in two successive years and sex ratios were female-biased, leading the author to conclude that survival over the maturation period was lower for females than males (Fincke 1982). Recapture and survival estimates correctly predicted sex ratios in mature *Coenagrion puella*, but not *Ischnura elegans*, which suggests that males have a lower survival rate than females in *I. elegans* over the maturation period (Anholt et al. 2001). In the zygopteran *Pyrrhosoma nymphula*, females do not have significantly different daily survival rates over sexual maturation, but take 6 days longer to mature, leading to lower survivorship (Bennett and Mill 1995). In the only study to examine phenotype selection over the maturation period, very large and small female *Enallagma boreale* individuals survived less well to maturity in both years of a two-year study and small males survived better in one year but not the other (Anholt 1991).

Large size at maturity is more important in males of territorial than non-territorial species (Anholt et al. 1991; Kasuya et al. 1997b; Tsubaki and Ono 1987) and they therefore gain more mass over the maturation period (Anholt et al. 1991). Fat reserves have are instrumental in winning territorial contests in male *Calopteryx maculata* (Marden and Waage 1990), while greater flight muscle mass in male *Plathemis lydia* leads to a higher probability of mating success (Marden 1989a). Among territorial males, territory winners usually realize a much higher number of copulations than losers (Fincke 1992; Gribbin and Thompson 1991a; Ito 1960; Lee and McGinn 1986; Miller 1983; Tsubaki and Ono 1987; Waage 1973) or those that choose alternative strategies (Plaistow and Siva-Jothy 1996). Territory winners are often larger than losers (Kasuya et al. 1997b; Tsubaki and Ono 1987), although there are exceptions (e.g., Gribbin and Thompson 1991a), and territorial males are often larger than satellite males (Fincke 1992; Marden and Waage 1990; Moore 1990).

Since there is no equivalent benefit to large size in males of non-territorial species, males of these species gain less mass than males of territorial species (Anholt et al. 1991). As a result, the difference between female and male mass gain is much larger in non-territorial species. If there is a fundamental trade-off between growth and survival, then mortality, and thus the opportunity for selection, should be relatively higher for females than males in non-territorial than territorial species over the maturation period. This hypothesis has not been explicitly tested.

After sexual maturity, odonates return to the emergence site and attempt to secure mating opportunities. Males spend most of their time at the rendezvous site attempting to acquire mates while females spend most of their time away from the pond and only return when they have a clutch of eggs and are ready to mate. This typically occurs every few days (Corbet 1999).

Since males and females inhabit different habitats after maturity, they are subject to different selective pressures. Females must actively forage to acquire resources to produce egg clutches, but they do so away from the pond where predation risks are likely lower. Males spend less time foraging because they need no resources to produce egg clutches, but they inhabit an environment that is rich with predators such as spiders, frogs, birds, and aquatic invertebrates that are attracted to the high density of odonate prey. As a result, males likely have a greater overall risk of mortality and survival should be lower.

Several studies found lower mature survival in females than males (Banks and Thompson 1985a; Bennett and Mill 1995; e.g., Bick and Bick 1961; Koenig and Albano 1987) while others found higher female survival (Robinson et al. 1983) or no measurable difference (e.g., Andres and Rivera 2001; Anholt 1997; Hafernik and Garrison 1986; Hamilton and Montgomerie 1989). Moreover, in a concurrent study of two damselfly species, female survival was lower (0.579) than male survival (0.812) in *Ischnura elegans* but no such difference was found in *Coenagrion puella* (Anholt et al. 2001).

Large size is important for males of territorial species because they must actively establish and defend territories against aggressive conspecifics. This requires energy in terms of fat reserves and flight muscle tissue (Marden and Waage 1990), but these resources can be gathered away from the pond and its associated risk of predation. Non-territorial males, by contrast, achieve mating success mainly by chance. They can increase the chance of encounters with females by remaining at the pond as long as possible, but this also increases predation risk. Further, while mating success in territorial species is at least in part determined by territorial success, in non-territorial species, longevity is the principal determinant of reproductive success (Anholt 1991; Fincke 1982, 1986, 1988, 1997; Michiels and Dhondt 1991; Stoks 2000). Therefore, I expect survival to be lower in males of non-territorial species after maturity and selection to be easier to detect.

In **Chapter 1**, I explore the interplay among body size, mating system and natural selection before and after maturity in *L. congener*, *L. disjunctus* and *S. pallipes.* I predict that survival over the maturation period should be lower in females than males, but the difference should be smaller in the territorial dragonfly, *S. pallipes.* Since mortality over this period should be higher in females, I expect to find stronger selection in females than males, but the difference should be greater in the non-territorial damselflies, *L. congener* and *L. disjunctus.* After maturity, I expect male survival to be lower than female survival but the difference should be greater in territorial species because selective pressures should be greater on male non-territorial than territorial species.

By using mark-recapture techniques that simultaneously estimate recapture and survival probabilities, I will be able to more accurately estimate survival over the pre-maturity and post-maturity stages of adult odonates and compare differences between sexes. Further, this methodology allows the construction of any linear model to test for the effects of individual covariates on survival. I will use this technique to test explicitly for survival selection on body size in *L.* congener, *L. disjunctus* and *S. pallipes.*

Sexual selection

Sexual selection is differential mating success relative to a measured trait. Body size has often been cited as an important trait in determining mating success in odonates (e.g., Andres et al. 2000; Anholt 1991; Cordero 1995; Fincke 1986; Grether 1996b; Harvey and Walsh 1993; Kasuya et al. 1997a; Koenig and Albano 1987; McVey 1988; Michiels and Dhondt 1991; Moore 1990; Stoks 2000). Many of these studies have found a benefit to large size in males (Conrad and Pritchard 1992; Cordero 1995; Harvey and Walsh 1993; Michiels and Dhondt 1991; Rivera et al. 2002). Indeed, a recent meta-analysis found directional sexual selection for large size in both non-territorial and territorial species, although it was stronger in territorial species (Sokolovska et al. 2000). If size is to be maintained over the long term, however, stabilizing selection, in which individuals near the mean trait value realize greater success than those in the tails of the distribution, should be the norm rather than directional selection (Thompson and Fincke 2002). In spite of this, only three studies, all on lifetime mating success in non-territorial males, have found stabilizing sexual selection on body size in odonates (Banks and Thompson 1985b; Fincke

1982, 1988; Stoks 2000), perhaps in part because large sample sizes are necessary to detect stabilizing selection.

Sexually mature males spend most of their time at the rendezvous site, but females only return occasionally when they have a mature clutch of eggs (Fincke 1988; Koenig and Albano 1987; Michiels and Dhondt 1991). As a result, the operational sex ratio (OSR) at the rendezvous site is typically highly male-biased (e.g., Anholt et al. 2001; Bick and Bick 1963; Cordoba-Aguilar 1994; Hamilton and Montgomerie 1989; Stoks 2001b). Most females mate, but many males do not (Bick and Bick 1961; Fincke 1982, 1988; Garrison 1978; Hafernik and Garrison 1986; Moore 1989), thus competition among males for access to females can be intense.

As noted above, odonate mating systems are diverse. *Lestes congener* and *L. disjunctus* males engage in scramble competition for females. Encounters with females occur mainly by chance and longevity plays an important role in determining lifetime reproductive success (Anholt 1991; Fincke 1982, 1986, 1988, 1997; Michiels and Dhondt 1991; Stoks 2000). If foraging is risky, or takes time away from mating, I would expect non-territorial males to forage only when necessary to maintain survival and reproductive potential. Since large size should not benefit males that engage in scramble competition, selection on body size should be relatively weaker and less likely than in territorial species. Indeed, where agility is advantageous, we might expect smaller males to have higher success (Crompton et al. 2003; Neems et al. 1992, 1998).

Males of territorial species, such as *S. pallipes* actively establish and defend territories against conspecific males. Within a territorial species, males may adopt alternative strategies, but they usually realize much lower mating success (Fincke 1992; Ito 1960; Miller 1983; Plaistow and Siva-Jothy 1996; Tsubaki and Ono 1987). Large size in territorial males has typically been found to confer greater mating success (Fincke 1984, 1992; Marden and Waage 1990; Moore 1990; Plaistow and Siva-Jothy 1996). However, large size may consequently have inescapable negative consequences because more active animals are at higher risk of predation (Abrahams and Dill 1989; Clutton-Brock 1989; Kohler and McPeek 1989; Magnhagen 1991; Peckarsky et al. 1993; Peckarsky et al. 2001; Rehfeldt 1992a). Since territorial males usually realize greater lifetime reproductive success than those that adopt alternative strategies, one can assume that the benefits of territoriality for large individuals outweigh the consequences. I therefore expect that sexual selection should favour large males in territorial species, although this must have limits relative to the effect of size on survival.

In **Chapter 2**, I examine the role of mating system on phenotypic sexual selection in the non-territorial damselflies, *L. congener* and *L. disjunctus* and the territorial dragonfly, *S. pallipes.* Since most females mate, sexual selection on body size is likely to be uninteresting and confounded by variation in mass due to the presence or absence of egg clutches. I therefore focus only on males in this chapter. I expect to find weak or non-existent sexual selection on body size in male *L. congener* and *L. disjunctus*, and selection for large size in male *S. pallipes.* Unpredictable variables such as weather can have large consequences on odonate activity (e.g., Michiels and Dhondt 1991; Rivera et al. 2002), and the form and direction of selection can change between episodes (e.g., Anholt 1991) making comparisons between studies problematic. No single study has compared sexual selection between territorial and non-territorial odonate species concurrently in the field in two successive years.

Further, selection can act in opposing directions between episodes (Schluter et al. 1991). For example, small size may decrease mating success, but increase longevity (e.g., Anholt 1991). While stabilizing selection may not occur within an episode, such as mating success, conflicting trade-offs between episodes may nonetheless act to keep body size consistent over time. By concurrently examining natural and sexual selection in three species of odonates, it will be possible to determine if overall selection is responsible for the maintenance of body size over time.

CHAPTER 1

EPISODIC NATURAL SELECTION IN ADULT MALES AND FEMALES OF TWO NON-TERRITORIAL DAMSELFLIES AND A TERRITORIAL DRAGONFLY

Introduction

Studies of natural selection in the wild illuminate the process of evolution by disentangling adaptations of organisms to their environment. The role of phenotype in determining fitness is affected by factors such as sex, mating behaviour and environmental influences. Differences in selection between the sexes can occur because males and females are subject to different selective pressures. Overall fitness is the sum of several selective episodes including survival to maturity, longevity, fecundity and mating success. Survival does not necessarily confer reproductive success. Natural and sexual selection can often act in opposing directions (Schluter et al. 1991), so that an individual with a particular combination of traits may be more likely to survive but less likely to reproduce. One must therefore separate various selection episodes in the life history of a cohort in the study of natural selection. Differences in phenotype distributions among years and generations can also have important influences on the form and direction of selection between successive episodes. Studies of selection that focus on the fitness of only one generation are a snapshot and may yield misleading conclusions about long-term evolutionary processes because selection can be affected by unpredictable variation in the environment.

Here, I consider natural selection to mean the change in phenotypic distributions within generations as a result of selective pressures (Endler 1986). Further, following Darwin (1859; 1871) and Endler (1986), I differentiate between natural selection, which is a result of selective pressures on mortality, and sexual selection, which is a result of differential mating success. Formal definitions of natural selection stress that heritability of traits is necessary for evolution to occur over generations (Endler 1986), but measurements of heritability can be conducted separately from measurements of selection. Lifetime reproductive success (LRS) is the fundamental measure of individual fitness, but it can be difficult or impossible to detect. By breaking LRS into its components, we can study the effects of variables such as behavior and morphology. Natural selection, through survival (and therefore longevity), and sexual selection, through mating success, are the two main components of LRS.

Components of fitness can be strongly affected by body size (mammals: Clutton-Brock 1989; birds: Price and Grant 1984; insects: Thornhill and Alcock 1983). In insects, large size (Blackmore and Lord 2000; Blanckenhorn et al. 2002; Honek 1993; Lauziere et al. 2000; Lefranc and Bundgaard 2000; Logan et al. 2001; Partridge 1988; Peckarsky et al. 1993; Preziosi et al. 1996; Sopow and Quiring 1998) and food intake (Blanckenhorn et al. 1995; Richardson and Baker 1997) can increase fecundity in females, and increase male territorial success (Fincke 1982, 1984, 1992; Moore 1990). Large size, however, can incur costs because mass gain and maintenance require active foraging that put an animal at greater risk of predation (Abrahams and Dill 1989; Abrams 1990, 1991; Kohler and McPeek 1989; Peckarsky et al. 1993). Predator avoidance through behavior modification is common among animals (e.g., Kohler and McPeek 1989; Lima and Dill 1990; McPeek 1990; Schaffner and Anholt 1998; Sih 1982; Skelly and Werner 1990; Stoks et al. 2003). Thus, there appears to be a fundamental trade off between growth and survival, with the effect that individuals should reduce foraging activity so that they reduce predation risk while maintaining an energy budget sufficient to survive and reproduce.

Odonata, including Suborders Anisoptera (dragonflies) and Zygoptera (damselflies), vary in mating behaviour, even among closely related species (Corbet 1999), and are therefore useful for the study of the relationship between mating behaviour and selection. Odonates are appropriate for natural selection studies because: 1) they tend to gather around small water bodies such as ponds for much of their adult life; 2) they can be observed throughout their short adult lifespan of 5-8 weeks (Corbet 1999), making estimates of lifetime survival and reproductive success possible; 3) they are large and therefore easy to mark and observe; 4) different species with distinct behavioral systems can be observed within the same habitat. Due to these characteristics, odonates have been the subject of several studies of natural and sexual selection (e.g., Anholt 1991; Cordero 1995; Fincke 1986; Grether 1996b; Harvey and Walsh 1993; Kasuya et al. 1997a; Koenig and Albano 1987; McVey 1988; Michiels and Dhondt 1991; Moore 1990; Stoks 2000).

Odonates have two distinct adult life-history stages. Eclosion occurs when the odonates emerge from the aquatic larval exoskeleton, during which time they are incapable of flight and at risk of predation and until their exoskeletons harden. Once the wings dry, they leave the place of emergence and do not return until sexually mature, a process that can take from several days to about two weeks (Corbet 1999). During this time, mass dramatically increases in most species, in some cases up to three times that of mass at emergence (Anholt et al. 1991).

The second adult stage begins at maturity when males return to the site of emergence and attempt to mate with returning females. Females typically return only when necessary to find mates and oviposit, but are otherwise absent from the breeding site. Once adults attain maturity, mass varies somewhat, but is relatively stable and tends to decrease slowly (Corbet 1999). This weight maintenance should require less frequent foraging.

It is evident that these adult life-history stages result in two important episodes of natural selection: survival during maturation and survival after sexual maturity. If there is a fundamental trade off between growth and survival, then selective pressures during these episodes should vary relative to growth. Since growth over the maturation period is much greater than after maturity, mortality should be higher before than after maturity and the opportunity for selection should consequently be higher. Further, mass gain patterns differ between male and female odonates. With few exceptions (e.g., Dunham 1993), females gain more mass over the maturation period than males, but the difference is smaller in territorial species than non-territorial species (Anholt et al. 1991). Correspondingly, females have been found to have lower survival than males over sexual maturation in at least three coenagrionid damselflies (Anholt 1991; Garrison 1978; Hamilton and Montgomerie 1989), one lestid damselfly (Bick and Bick 1961), and one libellulid dragonfly (Koenig and Albano 1987). Since mortality is higher in females over the maturation period, it follows that the opportunity for selection should also be stronger in females than males over this period.

Mating systems can also play a role in selection. Odonate species display a wide range of male mating systems from scramble competition to territoriality (Corbet 1999). This has implications for the importance of body size in males. Those engaging in scramble competition for females benefit from increased maneuverability and longevity (Anholt 1991; Crompton et al. 2003; Neems et al. 1998); large body size is thus not expected to play a critical role in lifetime reproductive success in males of these species. In fact, if growth increases predation risk, and large size is not beneficial in these species, then males might benefit from small size (Anholt 1991; Crompton et al. 2003; Neems et al. 1998).

Within territorial species, males can adopt either strictly territorial strategies or alternatives, including sneaking and satellite behaviour (Corbet 1999; Fincke 1985; Forsyth and Montgomerie 1987; Tsubaki and Ono 1986). Among territorial males, territory winners usually realize a much higher number of copulations than losers (Fincke 1992; Gribbin and Thompson 1991a; Ito 1960; Lee and McGinn 1986; Miller 1983; Tsubaki and Ono 1987; Waage 1973) or those that choose alternative strategies (Plaistow and Siva-Jothy 1996). Thus, there is strong selective pressure on males to be successful territory holders. In contrast to scramble competition strategies, territorial success is thought to depend on large body size in some odonate species. Males of territorial species gain more mass over the maturation period than males of non-territorial species (Anholt et al. 1991). Territory winners are often larger than losers (Kasuya et al. 1997b; Tsubaki and Ono 1987), although there are exceptions (Gribbin and Thompson 1991a), and territorial males are often larger than satellite males (Fincke 1992; Marden and Waage 1990; Moore 1990). If there is a trade-off between growth and survival, then males of territorial species may have lower survival over the maturation period than males of non-territorial species, but other differences among species make this a difficult comparison.

Lestes congener and *L. disjunctus*, like most zygopterans, are non-territorial (Bick and Bick 1961; Bick and Hornhuff 1965; Corbet 1999; Fincke 1982), displaying typical scramble competition for mates (Andersson 1994; Fincke 1982). Males at my study site typically displayed contact mate guarding, in which the male remains in tandem with the female during oviposition. In contrast, *Sympetrum* (Libellulidae: Anisoptera) are considered to be territorial, with some variation in intensity of territoriality among species (Fincke 1982; Michiels and Dhondt 1991; Ueda 1979; Van Buskirk 1986, 1987). *Sympetrum pallipes* males establish territories suitable for oviposition to attract females and actively defend them from conspecific males. *Sympetrum* males displayed both contact and non-contact mate guarding; females in this study were rarely observed ovipositing without a male present.

The objective of this study is to measure selection on the phenotypic characters, body size and wing loading, and its relationship to mass gain strategies before and after sexual maturity. I predict that mass gain during sexual maturation will be greater in females than males, but less so in *S. pallipes* due its territorial behavior. Further, I expect mass gain to be inversely correlated with survival with the result that survival should be lower before than after maturity and lower in females than males, but the difference should be smaller in *S. pallipes* than *L. congener* and *L. disjunctus*. After maturity, I expect males of non-territorial species to have relatively lower survival than males of territorial species. In addition, I expect survival to be lower in males than females after maturity because they spend much more time at the mating site, which is a predator-rich environment, often with little cover; thus they are potentially at higher risk of predation.

Longevity, and its corollary, survival, has been shown to be of principal importance as a component of lifetime reproductive success in male odonates (e.g., Anholt 1991; Fincke 1982, 1986, 1988, 1997; Stoks 2000). Since mating success is determined mainly by chance in males of non-territorial species, longevity in these species should presumably be of greater importance than in territorial species in which at least some of the opportunity for selection must be accounted for by territorial success. Results thus far are ambiguous: in non-territorial damselflies, longevity has been shown to account for 27 to 78% of the total opportunity for selection, including both sexual and natural selection (Banks and Thompson 1985b, 1987a; Fincke 1988; Marden 1989a), while in territorial species, it accounted for 27 to 57% (Koenig and Albano 1987; McVey 1988). However, a recent meta-analysis of the effect of body size in survival in odonates suggests that the mean effect size of directional selection on body size is much larger in males of territorial species ($z(r)= 0.27$, $P= 0.004$, $n= 3$) than males of non-territorial species ($z(r)= 0.047$, $P= 0.022$, $n= 7$).

The role of body size in fitness has been investigated in numerous studies (e.g., Arnqvist and Danielsson 1999; Blanckenhorn et al. 1998; Janzen et al. 2000; Nagel and Schluter 1998; Preziosi and Fairbairn 2000; Price and Grant 1984; Taylor et al. 1998), including several on odonates (Anholt 1991; e.g., Banks and Thompson 1985b; Cordero 1995; Fincke 1986; Grether 1996b; Koenig and Albano 1987; McVey 1988; Michiels and Dhondt 1991; Stoks 2000), but none have examined the role of mating system by measuring selection on body size in species with different mating systems concurrently in successive years. This study should allow a more comprehensive analysis of the role of body size in survival and its relationship with mating behaviour and differences between sexes. Further, with some exceptions (e.g., Anholt 1991; Anholt et al. 2001), estimates of survival in odonates have not taken into account the confounding effect of variation in recapture. Survival estimates are thus usually biased because it is never possible to catch all members of a population (Schmidt et al. 2002). This study will contribute to the understanding of true survival rates in adult odonates by concurrently estimating both survival and recapture.

Most studies of selection on body size assume that selection is uni-directional and test only for directional selection and not stabilizing or disruptive selection. But since most animals tend to maintain their body size over generations, with variation, overall stabilizing selection should be more common than directional selection. This can occur when selection between different episodes, such as survival and mating success, act in opposing directions, but it can also occur within one episode so that intermediate-sized individuals have greater fitness than those in the tails of the distribution. Sokolovska et al. (2000) found that large size was beneficial for longevity in female and male odonates of both territorial and non-territorial species, but tests for stabilizing selection were omitted. Few studies have tested for stabilizing selection on body size in odonates, in part because it requires large sample sizes. This study incorporates methodology that can simultaneously test for directional and stabilizing selection. In combination with a concurrent study on sexual selection on body size (Chapter 2), this will allow an examination of the effect of selection on body size, both within and between episodes.

Materials and Methods

Study site

I conducted the study at a small (~0.1 ha), semi-permanent, fishless pond within a 2 ha. grassy field on Galiano Island, B.C. There is an ~3m wide band of uncut vegetation surrounding the pond on three sides including mostly Poacea, Carex and Juncus, with occasional *Salix* and *Alnus*. On the fourth side, *Rubus discolor* covers a dyke, constructed approximately 35 years ago to create the pond. The dyke area abuts a mature *Acer macrophyllum* / *Abies grandis* / *Thuja plicata* forest. There is a small (~60m^2), treed island in the middle of the pond. The island does not have suitable habitat for oviposition and little odonate activity was observed there. The pond is connected via an ~10m long culvert to another pond of approximately the same size and age. The culvert joins the two at the narrow ends of the ponds. This area is shaded by trees and is not suitable as oviposition habitat. The closest suitable oviposition site at the adjacent pond is separated by about 25m from the study pond. No other ponds are closer than 2km from the study site.

Field observations

I made daily field observations from July 10 to September 7, and weekends from September 12 to 27 in 1998. In 1999, I made observations from July 12 to August 25, and weekends from September 1 to 20. Captures were made of both teneral (newly emerged adult) and sexually mature adult individuals. Strictly speaking, teneral refers to immediately post-emergent adults whose wings and exoskeletons have not yet dried, but I use it here to identify those individuals initially captured and released at emergence as opposed to those captured and released after maturity. Species were identified by morphological characteristics following Cannings and Stuart (1977). It was not possible to accurately age mature individuals; thus age is only known in tenerals. All observed tenerals were captured, but few were captured in 1998 (Table 1.2). Mature populations were too large to catch all individuals. Because the operational sex ratio at the pond was always male-biased, females were captured and marked preferentially. Because survival rates are based only on marked individuals, this preference does not bias survival or recapture estimates.

Odonates are not active during periods of poor weather; I therefore made no observations on these days (typically 1 to 2 days per week in 1998 and 2 to 3 days per week in 1999). I captured teneral and mature individuals upon first sighting. Due to the fragility of the exoskeleton, tenerals were not handled with fingers. Tenerals were captured in butterfly nets and transferred to 500mL plastic containers with mosquito netting-covered holes in both ends for ventilation. Each teneral was left in its own container overnight and marked, measured and released the following day, by which time their wings and exoskeletons were sufficiently hardened to allow handling.

After capture, I measured the wing and abdomen length of all individuals using stainless steel dial calipers ($\pm$0.01mm). For consistency, left rear wing measurements were always used where available. Right rear wing lengths were used when the left rear wing was damaged and used in subsequent analyses. If both rear wings were damaged, a front wing was measured, but not included in the analysis. Comparisons of repeated measurements of individuals showed that wing length measurements were slightly more consistent than abdomen length measurements, probably because abdomens were not always straight. I weighed all individuals using a Sartorius BP 110 electronic scale ($\pm$1mg). Each animal was given a unique mark consisting of four colored spots using Faber-Castell® paint pens: two on the left rear wing, one on the thorax and one on the abdomen. Six colors were used. In the first year, some colors, such as red, were found to fade with exposure to sunlight. These colors were replaced in 1999 with those that were found not to fade. Individuals for which color identification was uncertain were removed from the mark-recapture data set.

I created three separate marking groups based on the ease with which species and sex could be identified at a distance. These were *Lestes* (both *L. disjunctus* and *L. congener*) males, *Lestes* females and *Sympetrum pallipes*, including both males and females. After marking, individuals were released and all re-sightings were recorded. Odonates tend to congregate at or near the oviposition site (Corbet 1999) but not always; observations were therefore mainly made near the pond and occasional, but regular, forays were made away from the pond, although few odonates were captured.

Because I caught few tenerals in 1998 (Table 1.2), I raised some larvae in artificial aquaria in 1999. Two aquaria were constructed of plastic boxes (60 x 90cm) with mosquito netting placed over top and sticks and bricks placed inside to provide structure for emergence. Both aquaria were filled with pond water to 20cm depth, and *L. congener* larvae from the study site were placed in one aquarium while *S. pallipes* were placed in the other. To reduce the amount of time spent in the aquaria, only larvae that had inflated wing pads and therefore were ready to emerge (Corbet 1999) were captured from the pond. No food source was supplied as odonates do not feed immediately before emergence (Corbet 1999). Eighty-three *L. congener* were raised in the aquaria while 49 were captured at emergence at the pond. One hundred sixty-five teneral *S. pallipes* were released from the aquaria and 245 emerged from the pond.

Statistical methodology

Variable selection

Selection analyses require the choice of a metric trait(s) to correlate with fitness. I measured abdomen and wing length and mass, but all are highly correlated. This can create problems in regression analysis of selection (Lande and Arnold, 1983; Mitchell-Olds and Shaw, 1987). I therefore preformed a principal components analysis for each species*sex*year group to reduce the dimensionality of the data sets (Lande and Arnold, 1983; Schluter and Smith, 1986). The first principal component, PC1, was always strongly and positively related to body size measurements (Table 1.5), and was therefore used as my measure of body size. The remaining principal components were inconsistent, difficult to interpret, and therefore of little use in the selection analyses.

Since exoskeleton size is fixed at emergence, mass proportional to body size should be a good predictor of flight muscle tissue and fat reserves, which are important in extended foraging and mate-searching activities (Marden 1988; Marden and Rollins 1994; Marden and Waage 1990). Further, the proportion of mass to wing length (hereafter called wing loading) should likely have an effect on an individual's maneuverability (Crompton et al. 2003). I therefore chose to use not only overall body size (PC1 scores) but also wing loading (mass/wing length) as my predictor variables for fitness probabilities in all species.

Body size at emergence tends to decline over the season (Falck and Johansson 2000; Koenig and Albano 1987; Van Buskirk 1987). In this study, date of emergence was significantly related to body size at emergence in all groups where $n>40$ (e.g., male *L. congener*, 1999: n=68, r^2=0.163, P=0.001; male *S. pallipes*, 1999: n=208, r^2=0.397, P<0.0001,). In mature individuals, date of capture was related to body size (e.g., male *L. congener*, 1999: n=140, r^2=0.031, P=0.037,) and the probability of being captured while mating in about one-half of the groups (e.g., male *S. pallipes*, 1999: n=171, r^2=0.025, P=0.0415). Where the results were significant, individuals tended to be smaller and have lower wing loading values later in the season. Declining size over the season was taken to be the effect of declining size at emergence because size is fixed at emergence and mass did not decline with age (e.g., male *L. congener*, 1999:

n=22, r^2=0.003, P= 0.815), although the age of few individuals was known. Because of the effect of date on body size and wing loading, it was included in all models.

Body size comparisons between years

In addition to the above, I also performed principal component analyses on pooled data for both years for each species*sex group. This allowed me to compare PC1 values between years to determine if body size was consistent between years. I compared mean PC1 values using two-tailed t-tests.

Selection analysis on apparent teneral survival

I conducted an analysis of selection on the effect of body size on teneral survival using both cubic splines and logistic regression. All tenerals released were given a dichotomous outcome: seen again or not seen again. Those that were not seen again died, emigrated or survived and returned to the pond, but were not observed. If emigration and resighting are assumed to be non-selective, then those observed at the pond should be a random sample of those that survived. The comparison of these two groups gives an estimate of the effect of body size on survival, but only holds if emigration, if it occurs, is non-selective. Size-biased dispersal has been implicated in *Ischnura elegans* and *Coenagrion puella* (Conrad et al. 2002) and *Enallagma boreale* (Anholt 1990b) but was not found in another population of *C. puella* (Thompson 1991). Because emigration from the population changes the phenotype distribution, measures of selection are still valid if predictions of future phenotype distributions are desired. Since the closest known pond to the study site is greater than 2km away, emigration would appear unlikely in this population.

Selection curves were first estimated for body size for each teneral group with adequate sample sizes (see Table 1.2) using cross-validated cubic splines calculated by a program supplied by Dolph Schluter (GLMS, version 1, 1988). The cubic spline is a non-parametric approach to visualizing selection curves (Schluter 1988) that provides a more accurate estimate of the fitness function than linear or quadratic regression because it is not restricted to symmetrical shapes, and can therefore indicate the presence of local modes or dips (Brodie et al. 1995; Schluter 1988). It describes the expected fitness of alternative phenotypes, as opposed to the selection coefficients of Lande and Arnold (1983), which measure the effects of the fitness function on the phenotype distribution (Schluter 1988). Due to the effect of the date of emergence on body size, I first regressed PC1 and wing loading against date and then used the regression residuals as the phenotype estimates.

The cubic spline provides a visual estimate of selection unconstrained by specific statistical models, but does not provide estimates of the strength and direction of selection. To estimate the strength and direction of selection, I also performed logistic regressions on these data. Logistic regression is a more appropriate technique than multiple linear regression for survival data because they are binomial, and logistic regression constrains fitness predictions to fall between one and zero. Additionally, nonnormally distributed residuals invalidate traditional multiple regression and can falsely suggest nonlinear selection surfaces (Janzen and Stern 1998).

I tested for directional and variance selection on body size (PC1) and wing loading in all three species. The regression equations that best estimate these types of selection are linear and second-degree polynomial, respectively. I used two equation forms:

$$w_i \sim \alpha_0 + z_i\alpha_{i1} \text{ and } w_i \sim \alpha_0 + z_i\alpha_{i1} + z_i^2\alpha_{i2},$$

where w_i is predicted individual fitness, z_i is the measured trait of each individual (body size or wing loading), α_0 is the intercept and α_{i1} and α_{i2} are the logistic regression coefficients. The z_i^2 term tests for selection on variance; a large positive value of α_{i2} would suggest selection for phenotypic extremes (disruptive selection), while a negative result would suggest selection against the extremes (stabilising selection). To compensate for the effect of date on the traits, I included date as an independent variable, with or without an interaction term, in all models. The model set also included the null model and one with date as the only independent variable. This created a set of nine candidate models for each group (see Tables 1.8, 1.15 and 1.16 – not all models shown). Identical candidate model sets were used for the selection analyses of mature adult survival (see below).

Model selection

The best models were chosen based on the Akaike Information Criterion (AIC - Akaike 1973) which applies the principle of parsimony to choose the most appropriate model from a set of biologically relevant models (Burnham and Anderson 1998). The AIC uses the Kullback-Leibler discrepancy to measure the distance between the "true" model (i.e., if all parameters were known) and each candidate in a set of proposed models. The model with the lowest AIC value will be the best approximation of "truth". The AIC introduces parsimony by imposing a penalty based on the number of parameters estimated because too many will make a model unsuitable for inference.

A ΔAIC value is calculated by subtracting the AIC value of the best model from the model in question. The best model of the set will have a ΔAIC of zero, and those models with a ΔAIC greater than 4.0 are generally not considered useful in describing the data (Burnham and Anderson 1998). AIC weights give the relative support from the data for a particular model compared to other models in the candidate set. Values range from 0 ("worst" model) to 1 ("best" model), but the best model usually has an AIC weight well below 1 if other models also have some support (Burnham and Anderson 1998). This allows a relative comparison of the value of each model in a set of candidates. For example, if a model has an AIC weight of 0.40, we can say that it has twice the support of a model with an AIC weight of 0.20. The use of a variance inflation factor was unnecessary because the residual deviance divided by the degrees of freedom was always between 1.2 and 1.4. Burnham and Anderson (1998), however, recommend using the AICc criterion, which has an additional small sample correction term, when there are fewer than about 40 observations per parameter (n/K).

Where model selection did not identify a single best model, a weighted average of the coefficients was calculated over the set of models suitable for inference (Burnham and Anderson 1998: equation 4.6). Unconditional standard errors were calculated by following similar procedures with estimated standard errors (Burnham and Anderson 1998: equation 4.10), thus incorporating model selection uncertainty into parameter and variance estimates

Capture mark-recapture

Resighting rates often differ from survival rates because recapture rates are less than 100%. Resighting rates are not a good index of survival because of variation in catchability among groups. Most adult odonates are only present at the rendezvous site (in this case, the pond) when they are attempting to mate. Thus, if an individual is not resighted, it could either be dead or simply not at the pond. Capture mark-recapture allows the separation of recapture rates (the probability of recapturing an individual given that it is alive and present at a particular sampling occasion) from survival rates. This provides unbiased estimates of survival even if groups of individuals differ in their catchability. To achieve the most unbiased estimates of survival in these species, I therefore performed a mark-recapture analysis to investigate three questions: 1) do pre-reproductive and post-reproductive individuals have the same daily probability of survival; 2) do male and female survival rates differ; and 3) what is the effect of body size on survival probabilities? The last of these questions specifically addresses natural selection.

Resighting frequencies varied by species, sex and year (Table 1.1). To achieve the best estimates of survival and selection on body size, I created separate recapture data matrices for each species*sex*year group. When the number of teneral releases was adequate, each data set was divided into two groups to identify those individuals initially released as tenerals or mature insects; otherwise, both teneral and mature individuals were pooled into the same data set. This configuration resulted in a total of ten data sets (Table 1.1).

Table 1.1. Total number of individuals released per species in 1998 and 1999, with resighting rates (proportion of individuals re-sighted at least once after release) for each species*year group included in capture mark-recapture analyses.

group	Tenerals released	Teneral resighting rate	Mature released	Mature resighting rate	Groups included in analysis
1998					
Lestes congener female	45	0.29	178	0.25	Teneral + mature
Lestes congener male	36	0.19	224	0.41	Teneral + mature
Lestes disjunctus female	9	0	128	0.09	Mature only
Lestes disjunctus male	5	0	258	0.28	Mature only
Sympetrum pallipes female	8	0	176	0.12	Mature only
Sympetrum pallipes male	6	0.17	312	0.38	Mature only
1999					
Lestes congener female	70	0.09	0	0	Teneral only
Lestes congener male	63	0.24	0	0	Teneral only
Sympetrum pallipes female	211	0.10	47	0.17	Teneral + mature
Sympetrum pallipes male	199	0.22	67	0.50	Teneral + mature

Goodness of fit

Mark-recapture analyses begin with goodness of fit (GOF – Tables 1.2 and 1.3) tests to verify if mark-recapture assumptions have been met and to determine the fit of the model to the data (Lebreton et al. 1992; White and Burnham 1999). These assumptions include: *i.* equal survival probabilities among individuals within groups; *ii.* equal recapture probabilities among individuals within groups; *iii.* marks not lost or missed, and *iv.* instantaneous recapture relative to the recapture

Table 1.2. Goodness of fit results for Cormack-Jolly-Seber (CJS) time-dependent models for all *Lestes* groups with data pooled to weeks, 1998 and 1999. Data analyzed using program U-CARE (Choquet et al. 2001). Test 2.Ct and 2.CL test for the assumption of equal probability of recapture regardless of the time of initial capture; tests 3.SR and 3.SM test for equal probability of survival regardless of the time of initial capture (Cooch and White 2003).

test	X^2	*df*	*P*-value	X^2	*df*	*P*-value
			***Lestes congener*, 1998**			
		female			male	
teneral						
3.SR	5.180	3	0.159	0.582	2	0.748
transience	1.842	3	0.065	0.539	2	0.590
3.SM	0.787	1	0.375	0	2	1
2.Ct	1.490	2	0.475	0	2	1
trap-dependence	0.863	2	0.388	0	2	1
2.CL	0	1	1	0	2	1
mature						
3.SR	1.259	5	0.939	2.917	5	0.713
transience	0.261	5	0.794	0.156	5	0.876
3.SM	1.839	2	0.399	2.086	5	0.837
2.Ct	2.483	5	0.779	1.528	5	0.910
trap-dependence	0.439	5	0.660	0.415	5	0.678
2.CL	1.495	3	0.683	2.493	4	0.646
teneral + mature						
transience	1.335	8	0.182	0.420	7	0.675
trap-dependence	0.090	7	0.928	0.351	7	0.726
2+3	**14.534**	**22**	**0.881**	**9.607**	**26**	**0.999**
			***Lestes congener*, 1999**			
		female			male	
3.SR	2.479	1	0.115	0.936	1	0.333
transience	1.574	1	0.115	0.967	1	0.333
3.SM	0.936	1	0.333	N/A	N/A	N/A
2.Ct	0.708	3	0.871	0.424	5	0.995
trap-dependence	0.486	3	0.627	0.291	5	0.771
2.CL	0.708	3	0.871	1.335	5	0.931
2+3	**4.831**	**8**	**0.775**	**7.526**	**19**	**0.991**
			***Lestes disjunctus*, 1998**			
		female			male	
3.SR	0	4	1	2.340	6	0.886
transience	0	4	1	0.384	6	0.701
3.SM	N/A	N/A	N/A	0.881	4	0.927
2.Ct	0.936	4	0.919	4.971	5	0.419
trap-dependence	0.484	4	0.629	0.428	5	0.669
2.CL	N/A	N/A	N/A	5.068	4	0.280
2+3	**0.936**	**8**	**0.999**	**13.259**	**19**	**0.825**

interval. Violations of the assumptions can lead to poor fit, but assumptions *i* and *ii* can be tested using specially designed GOF tests.

GOF testing begins with the most parameterized model (White and Burnham 1999). In this case it was the fully time-dependent (CJS) model with separate survival and recapture estimates for each group in every interval. Data sets were separated into species*sex*year groups to form a total of ten analyses. The analyses were run with age class (marked as a teneral or mature individual, where data permitted) as a grouping factor, therefore generating one to two groups for each analysis. Recapture effort was daily, thus day was used as the recapture interval in the analyses. There was no recapture effort on days of poor weather (~1-2 days/week on average); these days were removed from the recapture histories and the length of the resultant interval was specified in MARK (White and Burnham 1999). For example, if two successive days were missed, they would be removed from the recapture histories and the resultant interval would be specified as three days. MARK estimates daily recapture and survival over this period even if the interval is longer than one day. This accommodates uneven recapture effort over the season because each interval, regardless of length, has one day of recapture effort. The number of days of recapture per group varied from 37 to 51, and the most parameterized models therefore included over 100 estimable parameters.

Goodness of fit results are presented in Tables 1.2 and 1.3. They indicated trap-dependence (happiness) in most male groups in both years, and transience in most teneral groups and in mature male *S. pallipes* (not shown here). In these groups, trap-dependence statistics were negative. This indicated that those individuals that were captured on the previous occasion were more likely to be captured than those that were not captured on the previous occasion. Since most "recaptures" were merely observations, trap-dependence did not occur in a literal sense. Rather, the pond can be thought of as the trap, and "trap-happiness" as "pond-happiness". A significant statistic shows that once at the pond, individuals tend to remain there.

The presence of transients indicates that more individuals than expected are never recaptured. In the teneral age group, transience could occur through non-random emigration or mortality. The presence of transients in mature male *S. pallipes* suggests non-random mortality or permanent emigration, though no other ponds are known within 2km of the study site.

Pradel (1993) offers a solution for trap-dependence that involves creating new recapture histories for every recapture, but it only compensates for trap-dependence on the first interval following release or capture. Further, due to multiple recapture histories for each animal, teneral survival is inestimable and constraining survival to be a function of individual covariates becomes impossible with available software.

Table 1.3. Goodness of fit results for CJS models for *Sympetrum pallipes* with data pooled to weeks, 1998 and 1999. Data analyzed using program U-CARE (Choquet et al. 2001). Test 2.Ct and 2.CL test for the assumption of equal probability of recapture regardless of the time of initial capture; tests 3.SR and 3.SM test for equal probability of survival regardless of the time of initial capture (Cooch and White 2003).

test	X^2	*df*	*P*-value	X^2	*df*	*P*-value
			***Sympetrum pallipes*, 1998**			
		female			male	
3.SR	0	4	1	7.854	8	0.448
transience	0	4	1	1.083	8	0.279
3.SM	N/A	N/A	N/A	2.951	6	0.815
2.Ct	0.936	5	0.968	18.588	6	0.005
trap-dependence	0.433	5	0.665	3.834	6	0.0001
2.CL	1.667	4	0.797	3.697	6	0.718
2+3	**2.603**	**13**	**0.999**	**33.091**	**26**	**0.159**
			***Sympetrum pallipes*, 1999**			
		female			male	
teneral						
3.SR	0	1	1	0.676	2	0.713
transience	0	1	1	0.815	2	0.415
3.SM	N/A	N/A	N/A	0	1	1
2.Ct	1.111	2	0.574	0.132	2	0.936
trap-dependence	0.745	2	0.456	0.256	2	0.798
2.CL	6.272	5	0.281	0	1	1
mature						
3.SR	0.626	4	0.960	6.043	3	0.110
transience	0.378	4	0.705	2.216	3	0.027
3.SM	0.097	3	0.992	0.708	3	0.871
2.Ct	12.094	5	0.034	11.268	5	0.046
trap-dependence	0.741	5	0.459	1.347	5	0.178
2.CL	10.733	6	0.097	7.744	7	0.356
teneral + mature						
transience	0	5	1	1.162	5	0.245
trap-dependence	0	7	1	1.499	7	0.134
2+3	**3.919**	**8**	**0.864**	**27.578**	**24**	**0.278**

Pooling recapture occasions offers a more viable alternative for analyzing these data. To accomplish this, I summarized the capture histories for each individual over a multiple-day interval and assigned a 1 to those seen at least once during that week and a 0 to those never seen. I chose one week because it divided the season into intervals that were broad enough to increase the likelihood that the parameters would be estimable and specific enough to provide information on time structure of the model. This configuration also allowed the use of the data collected only on weekends in September, which would otherwise be too sparse to estimate daily survival accurately. Using this methodology, repeated captures would be less likely to show up as trap-dependence because they are more likely to fall within a one week period. Multiple recaptures could still span more than one week interval, but the occurrence of trap-dependence should be much less likely. With data pooled to weeks, the total number of sampling intervals per group for each season ranged from nine to eleven.

Overall goodness of fit tests (tests 2+3, Tables 1.2 and 1.3) showed that weekly recapture summaries did not have any significant lack of fit to the CJS model, but there is still a systematic lack of fit in test 2.Ct results in female *S. pallipes* in 1999 and in male *S. pallipes* in both years (Table 1.3), indicating that trap-dependence is still a problem. However, trap-dependence statistics changed sign from negative to positive when data were pooled, indicating that individuals in the pooled data were now less likely to be seen if they had been seen in the previous interval. Due to lack of fit from these model components, the ITEC model (Pradel 1993) was used to reduce bias in survival estimates in these groups. Since the ITEC model does not allow for the use of individual covariates, two analyses were conducted for these groups – with ITEC to derive the least biased survival estimates and without ITEC to determine the effect of individual covariates on survival estimates.

The sum of the 2.Cl, 3.Sr and 3.Sm chi-square tests are considered a goodness of fit test for the ITEC model (Cooch and White 2003; Pradel 1993). The results indicate a better fit for the ITEC models over the CJS models in male *S. pallipes* and a roughly equivalent fit in female *S. pallipes* (male *S pallipes*, 1998 – x^2=14.502, df=20, *P*-value= 0.797; female *S. pallipes* 1999 - x^2=11.821, df=18, *P*-value= 0.850; male *S. pallipes*, 1999 - x^2=15.171, df=17, *P*-value= 0.584); thus showing the ITEC models are appropriate for estimating adult or mature survival in these groups. However, because ITEC models create a new individual recapture history following each recapture, it was not possible to estimate teneral survival using these models.

An important assumption of mark-recapture studies is that marking does not reduce survival probabilities of individuals. "Marking effect" rates (where individuals disappear directly after marking) of 20 to 52% have been reported in odonates (Fincke 1988; Koenig and Albano 1987; McVey 1988) while others have reported no marking effect (Plaistow and Siva-Jothy 1996). I tested for apparent marking effect by comparing capture mark-recapture models with constant survival with those that have a separate estimate for the first interval following release. I tested these models in four groups only because they had the most mature releases and the highest recapture rates and should be the easiest groups in which to find a marking effect. Results were compared using the AICc criterion.

Model notation

Model notation followed Lebreton *et al.* (1992), with survival and recapture parameters identified as: Φ_i = apparent survival (hereafter survival), the probability that an individual seen at time *i* is alive and present at time *i* + 1; p_i = probability that an individual is sighted at time *i*, given that it is alive and present in the study area during time *i*. Both Φ and p can be estimated by MARK simultaneously with or without linear constraints such as environmental conditions or individual metric traits. Model subscripts identify structure. $\Phi_{(\cdot)}$, $\Phi_{(t)}$, $\Phi_{(a)}$, $\Phi_{(g)}$ and $\Phi_{(g*t)}$ indicate constant, time-dependent, age-dependent (i.e., teneral vs. mature), constant over time but with differences between groups and time-dependent survival with differences between groups, respectively. A model in which survival and recapture are constant over time would use the notation $\Phi_{(.)}$ $p_{(.)}$, and a model in which separate survival and recapture parameters are estimated for every interval would use the notation $\Phi_{(t)}$ $p_{(t)}$.

Model structure considerations

Several possibilities were available for modeling survival and recapture probabilities in both teneral and mature individuals. In teneral groups, survival and recapture could be modeled as constant over time, varying with time or varying with age (Table 1.3). I therefore created age-dependent models in which pre-reproductive survival and recapture was allowed to differ from post-reproductive estimates.

The duration of the prereproductive period typically varies between about two and ten days in zygopterans and about eight and twenty days in anisopterans (Corbet 1999). The duration of this period is not known for the species in this study; consequently I estimated it to be one or two weeks. This broadly agreed with the observed age of first recapture. Of all species, two individuals were captured at or before six days after release, but almost all (82/85) teneral recaptures occurred after 12 days. I used the subscript $_{(a=1)}$ to designate models in which there are two estimates for survival: one for the first capture interval and one for all the following intervals (Table 1.3). Similarly, a model with the subscript $_{(a=2)}$ would indicate one in which there is one constant estimate of survival over the first two capture intervals and one constant estimate over all following intervals. When both teneral and mature groups were combined in an analysis, parameter indices are separated by a forward slash. Thus, a model with constant teneral survival and time-dependent mature survival would be designated as $\Phi_{(./t)}$.

The survival and recapture structure used in analyses for both teneral and mature groups are shown in Table 1.4. Each survival structure was combined with each recapture structure to form the set of candidate models, with the exception that the teneral period, if specified, was equivalent in length between survival and recapture. Hence, $\Phi_{(a=1/.)}$ could be combined with $p_{(a=1/.)}$, but not $p_{(a=2/.)}$. This created a candidate set of 25 models in analyses with tenerals only, four models in mature only analyses and 64 models when tenerals and mature were included in the same analysis.

Table 1.4. Survival and recapture parameters incorporated in models. The total number of models was 25 for teneral groups, four for mature groups and 56 when the two groups were combined. The teneral group contains individuals initially released one day after emergence; the mature group is formed of individuals initially captured after sexual maturity (see text for details).

mature		teneral		teneral+mature	
survival	recapture	survival	recapture	survival	recapture
$\Phi_{(\cdot)}$	$p_{(\cdot)}$	$\Phi_{(\cdot)}$	$p_{(\cdot)}$	$\Phi_{(\cdot)}$	$p_{(\cdot)}$
$\Phi_{(t)}$	$p_{(t)}$	$\Phi_{(t)}$	$p_{(t)}$	$\Phi_{(t)}$	$p_{(t)}$
		$\Phi_{(a)}$	$p_{(a)}$	$\Phi_{(g)}$	$p_{(g)}$
		$\Phi_{(a=1)}$	$p_{(a=1)}$	$\Phi_{(g*t)}$	$p_{(g*t)}$
		$\Phi_{(a=2)}$	$p_{(a=2)}$	$\Phi_{(a=1/.)}$	$p_{(a=1/.)}$
				$\Phi_{(a=1/t)}$	$p_{(a=1/t)}$
				$\Phi_{(a=2/.)}$	$p_{(a=2/.)}$
				$\Phi_{(a=2/t)}$	$p_{(a=2/t)}$

Model structure has important implications for the number of potentially estimable parameters. If survival and recapture are constant over time, then only two parameters are estimated (one for survival and one for recapture). If there are 10 encounter occasions and both survival and recapture are modeled as time-dependent, the number of estimable parameters increases to 19 (the survival and recapture parameters over the last period are not separately estimable and the estimate provided by MARK is a product of survival and recapture over this period). Using two groups doubles the number of parameters in a model; $\Phi_{(g*t)}$ has twice the number of parameters as $\Phi_{(t)}$. Data are often too sparse to simultaneously estimate numerous parameters. For example, most teneral data sets, with the exception of male and female *S. pallipes* in 1999, could not support time-dependence because too many parameters were specified in the model. When sample sizes were small, (teneral male and female *L. congener* in both 1998 and 1999) I specified no time dependence in teneral survival or recapture estimates. This reduced the number of potential models in these groups from 64 to 36.

Further structure can be applied to the above models to reduce the number of parameters that need to be estimated. Survival or recapture can be constrained by any linear model. For example, recapture effort was not constant over the season. I therefore constrained recapture to be a linear function of the recapture effort for that week (# days of observation / week). Furthermore, odonate activity is weather-dependent; hence, survival or recapture can also be constrained by temperature (estimated as mean weekly temperature in °C – Measured at Galiano North weather station, data supplied by Environment Canada). Constraining survival to be a linear function of time is also possible and allows time variance in survival, but involves fewer parameters than time-dependence models. Following the initial run of candidate models, then, I chose the best models based on AICc and constrained recapture to be a linear function of effort or time and survival to be a linear function of weather or time. The best overall model was then chosen on the basis of AICc and used for inference.

The best model was chosen from among these models, with or without recapture effort, weather or time constraints. Survival estimates of these best models were further constrained to be a function of body size (PC1) or wing loading (mass (mg)/ wing length (mm)). This allows an estimate of the effect of body size or wing loading on survival. MARK provides beta parameters that are equivalent to logistic regression slopes and estimate the effect of each linear constraint in the model on the parameters they constrain. The beta parameters can then be transformed following the methods of Janzen and Stern (1998) so that they are directly comparable to selection gradients of Lande and Arnold (1983), often used in evolutionary studies.

Selection analyses on mature adult survival

To test for linear or variance selection on PC1 or wing loading, I constrained survival with the same nine models specified used for teneral survival selection. Each slope and interaction term included in the linear model increased the number of parameters of the model by 1. When the best unconstrained model included group (i.e., teneral / mature) or time effects, covariate*group or covariate*time interaction terms were included in the model. This increases the number of model parameters by a factor of two (group effects model) or t-1 parameters (time-dependent model, where t = number of recapture occasions). Models with interaction terms often had poor estimability due to small teneral numbers. In these cases, I compared interaction models with additive models (which require fewer parameters) using likelihood ratio tests and AIC, then proceeded with additive models only if the interaction terms did not provide improved fit or increase the number of estimable parameters.

Some parameters were inestimable, especially in more complex models. These parameters are reported by MARK as having a value of one and a standard error of zero, or a value of zero with very large standard errors. When this was encountered, these parameters were fixed at a value other than one or zero and the models were re-run; if the model deviance did not change, it confirmed that they were inestimable. In some groups, few parameters were found to be inestimable and the identity and number were consistent over models with and without linear constraints. The relative ranking of the models was therefore not affected and parameter numbers (K) were not adjusted in AICc weight calculations (Table 1.9). In other groups, where the number of inestimable parameters was too large or the identities of inestimable parameters were inconsistent among models, K was adjusted. This process eliminated models from consideration that were too complex given the data. When using linear models to constrain survival with body size covariates, I always included the additional parameters when calculating AICc, whether they were reported by MARK or not. Thus, model comparison was consistent, even when some beta parameters were inestimable.

Results

Principal components analysis

Abdomen length, wing length and mass all had similar strong positive loadings on PC1 (Table 1.5). PC1 accounted for between 48 (male *L. disjunctus*, 1998) and 77% (female *S. pallipes*, 1999) of the variance in the whole data set. PC1 is thus a good measure for overall body size.

Table 1.5. Principal Component 1 (PC1) scores, 1998 and 1999 with principal component standard deviations and the proportion of variance accounted for by PC1, as well as mean wing loadings values ± standard deviation. Trait values, other than wing loading, represent loadings on phenotypic characters. Separate PC analyses were run for each species*sex*year group.

	Loadings on PC1				proportion of variance	
	Abdomen	Wing	Mass	standard deviation	accounted for by PC1	wing loading (mg/mm)±SD
Lestes congener						
female, 1998	0.51	0.58	0.64	1.31	0.57	3.01 ± 0.39
female, 1999	0.53	0.62	0.58	2.09	0.70	3.24 ± 0.32
male, 1998	0.62	0.51	0.61	1.37	0.63	2.06 ± 0.17
male, 1999	0.48	0.65	0.60	2.05	0.68	2.30 ± 0.24
Lestes disjunctus						
female, 1998	0.59	0.60	0.54	1.41	0.66	3.24 ± 0.38
female, 1999	0.57	0.56	0.60	2.28	0.76	3.28 ± 0.41
male, 1998	0.57	0.42	0.71	1.21	0.48	2.34 ± 0.20
male, 1999	0.61	0.53	0.59	2.09	0.70	2.35 ± 0.19
Sympetrum pallipes						
female, 1998	0.62	0.54	0.57	1.41	0.66	8.64 ± 1.01
female, 1999	0.59	0.59	0.56	2.32	0.77	8.20 ± 0.94
male, 1998	0.56	0.56	0.60	1.38	0.64	6.90 ± 0.59
male, 1999	0.57	0.54	0.63	1.39	0.65	6.73 ± 0.60

Size differences between years

Male and female *L. congener* and female *S. pallipes* were smaller at emergence in 1998 than 1999; male *S. pallipes* had larger wing loading values at emergence in 1998, but overall body size was not significantly different (Table 1.6). After maturity, all *Lestes* groups, except male *L. disjunctus*, which was narrowly non-significant at $P = 0.052$, were significantly larger in 1999 than in 1998, and both male and female *S. pallipes* were significantly smaller in 1999 than in 1998

(Table 1.6). Mass was greater relative to wing length in *L. congener* in 1999 than 1998 while in *S. pallipes*, the reverse was true. Wing loading values were consistently higher in females than males, but the difference was not statistically tested (Table 1.6).

Table 1.6. Comparison of mean body size residuals between years for all species*sex groups. PC1 is the first principal component of the correlation matrix of abdomen and wing lengths and mass for two years' combined data for each group corrected for date. Standard deviations are for two years' pooled data. Proportional change (prop. change) is 1999 mean – 1998 mean divided by the standard deviation.

	1998	*1999*	*std. dev.*	*prop. change*	*t*	*P*	*df*
Lestes congener							
female teneral							
PC1	-1.32 ± 1.21	0.80 ± 1.04	1.51	1.41	-10.14	<0.0001	117
wing loading	-0.18 ± 0.20	0.11 ± 0.18	0.23	1.26	-7.89	<0.0001	117
female mature							
PC1	-0.62 ± 1.25	0.59 ± 1.28	1.40	0.87	-9.35	<0.0001	378
wing loading	-0.07 ± 0.40	0.07 ± 0.31	0.36	0.39	-3.81	0.0002	378
male teneral							
PC1	-1.23 ± 1.18	0.63 ± 1.22	1.49	1.25	-7.36	<0.0001	99
wing loading	-0.18 ± 0.17	0.09 ± 0.17	0.21	1.59	-7.85	<0.0001	99
male mature							
PC1	-0.50 ± 1.14	0.79 ± 1.45	1.42	0.91	-9.50	<0.0001	365
wing loading	-0.07 ± 0.18	0.11 ± 0.26	0.23	0.78	-7.88	<0.0001	365
Lestes disjunctus							
female mature							
PC1	-0.14 ± 1.28	0.47 ± 1.81	1.44	0.42	-2.31	0.022	161
wing loading	-0.02 ± 0.38	0.06 ± 0.39	0.21	0.39	-1.06	0.291	161
male mature							
PC1	-0.07 ± 1.18	0.27 ± 1.51	1.26	0.27	-1.95	0.052	317
wing loading	-0.01 ± 0.20	0.04 ± 0.19	0.20	0.25	-2.11	0.036	317
Sympetrum pallipes							
female teneral							
PC1	-2.01 ± 1.89	0.07 ± 1.28	1.36	1.60	-4.44	<0.0001	223
wing loading	-0.77 ± 0.36	0.03 ± 0.43	0.46	1.74	-5.15	<0.0001	223
female mature							
PC1	0.47 ± 1.28	-0.61 ± 1.40	1.43	0.75	7.07	<0.0001	309
wing loading	0.10 ± 1.01	-0.13 ± 0.93	0.98	0.23	1.98	0.048	309
male teneral							
PC1	0.36 ± 2.68	-0.01 ± 1.14	1.20	0.31	0.74	0.461	211
wing loading	0.60 ± 1.81	-0.02 ± 0.41	0.50	1.24	3.02	0.003	211
male mature							
PC1	0.36 ± 1.28	-0.64 ± 1.28	1.37	0.73	8.32	<0.0001	487
wing loading	0.02 ± 0.57	-0.03 ± 0.60	0.59	0.08	0.87	0.386	487

Mass gain from emergence to sexual maturity

Lestes females gained between 38 and 98% of their mass at emergence over the maturation period, while males gained between 6.2 and 33.2% (Table 1.7). In *S. pallipes*, females gained 223% in 1998 and 127% in 1999 while males gained 52 and 66%, respectively. Female mass gain was consistently at least double that of males over this period for each species in both years (Table 1.7).

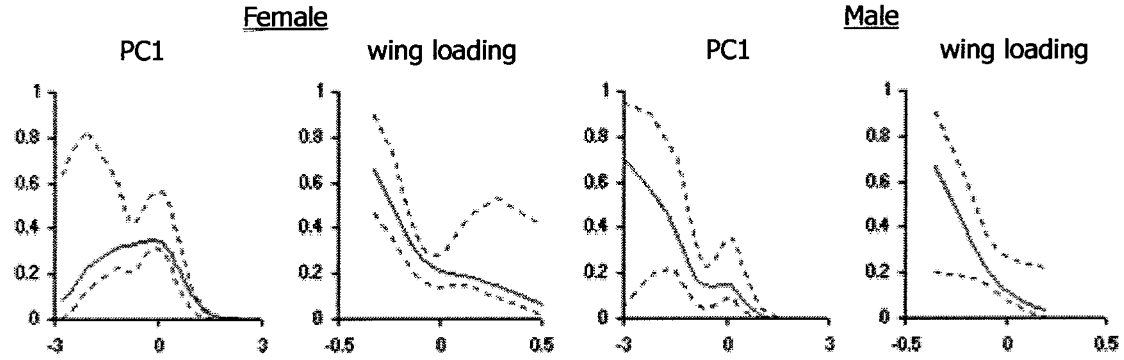
Table 1.7. Comparison of mass at emergence and sexual maturity, 1998 and 1999. Values are mean mass per group, ± standard deviation. *n* shows the total number of individuals per group at emergence and sexual maturity, respectively. Proportional mass gain is (mature mass – emergent mass) / emergent mass.

	mass (mg)		
	emergence	*maturity*	*proportional mass gain*
Lestes congener			
female, 1998 (*n* = 45 / 186)	34.00 ± 4.16	63.37 ± 9.11	0.981
female, 1999 (*n* = 75 / 195)	42.35 ± 4.55	71.98 ± 8.39	0.700
male, 1998 (*n* = 34 / 226)	30.44 ± 3.24	40.51 ± 3.83	0.332
male, 1999 (*n* = 68 / 144)	38.07 ± 4.34	47.67 ± 6.37	0.252
Lestes disjunctus			
female, 1998 (*n* = 9 / 127)	42.00 ± 9.03	71.09 ± 9.19	0.740
female, 1999 (*n* = 8 / 38)	52.62 ± 1.43	72.82 ± 10.66	0.384
male, 1998 (*n* = 5 / 254)	36.25 ± 5.12	47.77 ± 4.17	0.318
male, 1999 (*n* = 6 / 67)	45.83 ± 4.71	48.69 ± 4.43	0.062
Sympetrum pallipes			
female, 1998 (*n* = 8 / 176)	71.25 ± 12.33	229.76 ± 28.77	2.225
female, 1999 (*n* = 217 / 136)	91.29 ± 14.48	207.28 ± 27.78	1.271
male,1998 (*n* = 6 / 311)	122.00 ± 49.82	185.77 ± 17.84	0.523
male, 1999 (*n* = 208 / 182)	103.68 ± 9.24	172.30 ± 17.64	0.662

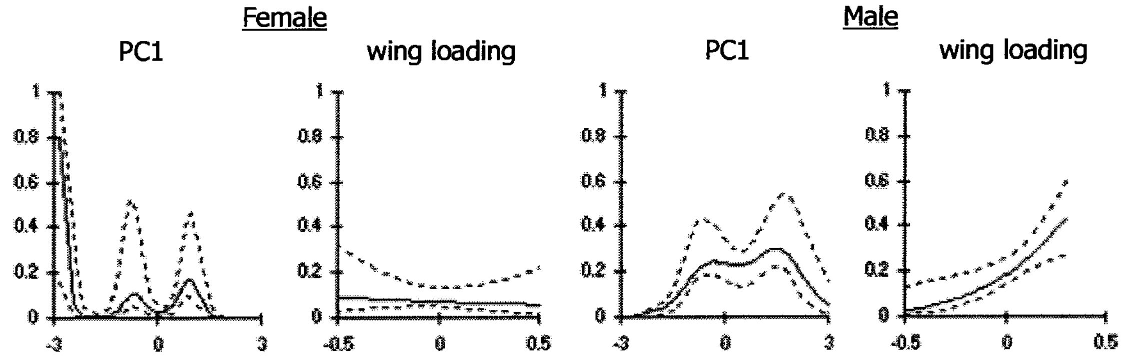
Teneral survival selection

There was strong evidence of survival selection on body size in teneral *L. congener* males and females in 1998, but none in 1999. In *S. pallipes*, there was no evidence of selection in females but very strong evidence in males (Figure 1.1, Tables 1.8 and 1.9).

***Lestes congener*, 1998**



***Lestes congener*, 1999**



***Sympetrum pallipes*, 1999**

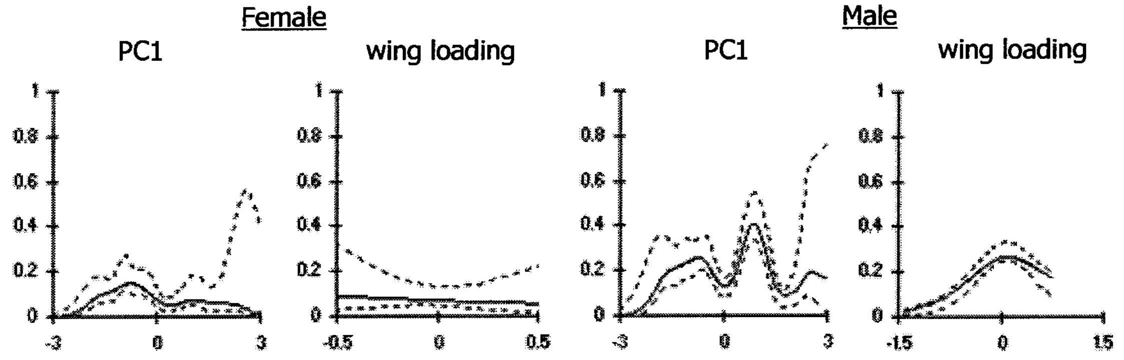


Figure 1.1. Cubic spline selection curves estimating expected survival to maturity as predicted by overall body size (PC1), wing loading at emergence, 1998 and 1999. x-axes represent PC1 or wing loading values (mg/mm), all corrected for date; y-axes represent expect survival probabilities. Solid curves are the best estimates of the selection curves; dashed lines are 95% bootstrapped confidence intervals (r=10,000). GLMS program provided by Dolph Schluter (1988).

In female *L. congener*, there was apparent stabilizing selection on PC1 in 1998 and possible disruptive selection in 1999. Although they were smaller in 1998 (Table 1.6), females with very large PC1 scores appeared to survive less well (Figure 1.1); the selection curve suggests a similar decrease for very small individuals, but the confidence intervals to are too wide to draw reliable conclusions. Thus, the overall effect on body size could be stabilizing or negative directional. In 1999, there is a decrease in survival probabilities for individuals with mean body size and a relative increase for slightly larger and smaller individuals (Figure 1.1), suggesting that disruptive selection may be acting on body size. Logistic regression results give some support to selection on body size in females in 1998 (Table 1.8 - Null model ΔAICc=0.99; evidence ratio for selection = 4.9), but transformed selection gradients are all small relative to standard errors (Table 1.9). There was no difference in PC1 residuals between those that were seen again (survivors) and those that were not in 1998 ($t = 1.433$, $df = 43$, p-value = 0.159) or 1999 ($t = 1.052$, $df = 72$, p-value = 0.297).

Wing loading provides no additional predictive power because models with wing loading did slightly worse than models with PC1, given a particular structure. There was no difference in wing loading residuals between survivors and those never seen again in 1998 ($t = 1.231$, $df = 43$, p-value = 0.225) or 1999 ($t = 0.248$, $df = 72$, p-value = 0.805). Survivors had a later mean date of emergence in 1998 (Julian date = 21.2) than those that were never seen again (Julian date = 15.8), but the difference was narrowly non-significant ($t = -1.8757$, $df = 43$, p-value = 0.0675); this difference was not apparent in 1999.

Male *L. congener* were smaller in 1998 than 1999, but there is clear evidence of negative directional selection on body size in 1998 and stabilizing selection in 1999 (Figure 1.1). Logistic regression results strongly suggest phenotypic selection in 1998 (Table 1.8 – Null model ΔAICc=3.32; evidence ratio for selection = 8.3), but not in 1999 (Null model ΔAICc=0). Transformed selection gradients are again small relative to standard errors, however, and confidence intervals overlap zero (Table 1.9). Cubic splines show negative directional selection on wing loading in 1998 and positive directional selection in 1998 (Figure 1.1), but no wing loading model was better than the null in either year (Table 1.8)

Table 1.8. AIC results for pre-maturity survival logistic regression selection analyses including model likelihood (-2log(L)) and number of parameters (K). Lowest AICc values indicate the models with the best fit, given the number of parameters. ΔAICc values represent the difference in AICc units from the best model. AICc weights designate the relative inferential value of each model; larger weights indicate greater support for the model. Only models with a ΔAICc value to and including ≥4.0 are shown.

Rank		*-2log(L)*	*K*	*AICc*	*ΔAICc*	*AICc weight*	*cumulative AICc weight*
	Lestes congener **female, 1998**						
1	Date	49.01	2	53.30	0	0.19	0.185
2	PC1+Date	46.77	3	53.35	0.06	0.18	0.365
3	wl+Date	46.89	3	53.48	0.18	0.17	0.534
4	Null	52.19	1	54.29	0.99	0.11	0.647
5	PC1+PC1^2+Date	45.77	4	54.77	1.48	0.09	0.736
6	wl+wl^2+Date	46.37	4	55.37	2.07	0.07	0.802
7	PC1+Date+PC1*Date	46.56	4	55.56	2.26	0.06	0.862
8	wl+Date+wl*Date	46.66	4	55.66	2.36	0.06	0.919
9	PC1+PC1^2+Date+PC1*Date	44.20	5	55.74	2.44	0.05	0.973
10	wl+wl^2+Date+wl*Date	45.62	5	57.16	3.86	0.03	1.000
	Lestes congener **female, 1999**						
1	Null	41.65	1	43.70	0	0.50	0.503
2	Date	41.75	2	45.92	2.22	0.17	0.669
3	PC1+Date	40.49	3	46.84	3.13	0.11	0.774
4	wl+Date	41.53	3	47.88	4.17	0.06	0.837
	Lestes congener **male, 1998**						
1	PC1+Date	23.69	3	30.49	0	0.47	0.468
2	PC1+PC1^2+Date	23.53	4	32.91	2.42	0.14	0.607
3	PC1+Date+PC1*Date	23.55	4	32.93	2.43	0.14	0.745
4	Null	31.69	1	33.81	3.32	0.09	0.834
5	wl+Date	28.32	3	35.12	4.63	0.05	0.880

Comparisons of traits between those never observed again with those that were support evidence of selection in 1998: mean PC1 residuals of survivors were much smaller (t = 2.998, df = 32, p-value = 0.005) and wing loading residuals were smaller, but non-significant (t = 1.7372, df = 32, p-value = 0.092).

There was no evidence for teneral survival selection on body size in female *S. pallipes*, except for a possible small peak in survival probabilities for PC1 values slightly smaller than the mean (Figure 1.1). Logistic regression results (Table 1.8) and transformed selection gradients (Table

1.9) further support lack of selection in this group. Further, there was no difference in teneral body size between those observed to have survived and those never seen again.

Table 1.8 continued.

Rank		-2log(L)	K	AICc	AAICc	AICc weight	cumulative AICc weight
	Lestes congener **male, 1999**						
1	Null	68.68	1	70.75	0	0.32	0.319
2	wl+Date	65.25	3	71.63	0.89	0.20	0.523
3	wl+Date+wl*Date	64.40	4	73.05	2.30	0.10	0.624
4	PC1+Date	66.95	3	73.33	2.58	0.09	0.712
5	Date	69.07	2	73.26	2.51	0.09	0.802
6	wl+wl^2+Date	65.22	4	73.87	3.12	0.07	0.869
7	PC1+PC1^2+Date	66.11	4	74.75	4.01	0.04	0.953
	Sympetrum pallipes **female, 1999**						
1	Null	137.98	1	140.00	0	0.36	0.360
2	Date	136.65	2	140.70	0.70	0.25	0.614
3	wl+Date	136.34	3	142.45	2.45	0.11	0.720
4	PC1+Date	136.55	3	142.67	2.66	0.10	0.815
5	PC1+PC1^2+Date	136.11	4	144.30	4.30	0.04	0.857
	Sympetrum pallipes **male, 1999**						
1	wl+wl^2+Date	204.33	4	212.52	0	0.67	0.672
2	wl+wl^2+Date+wl*Date	203.90	5	214.20	1.67	0.29	0.963
3	Null	219.30	1	221.32	8.79	0.01	0.980

In male *S. pallipes*, however, there was very strong support for selection on both body size and wing loading (Figure 1.1, Tables 1.8 and 1.9). The PC1 selection curve has two modes, just above and below mean body size, and two dips, one at mean body size, the other at very large body size (Figure 1.1). AIC values for the null and the best PC1 model are nearly identical, however, suggesting no selection on overall body size (Table 1.8). Given the shape of the curve in figure 1. 1, it would likely take a more complex regression model to find significant selection on body size in this group. The most convincing selection curve is on wing loading in this group (Figure 1.1). There appears to be strong positive directional and very strong stabilizing selection on wing loading values; this is confirmed by logistic regression results (Table 1.8) and transformed selection gradients (Table 1.9). The effect of date is complex because of the vagaries of weather. This could generate dips and other odd shapes in the teneral survival curves.

Table 1.9. Transformed body size selection gradients with standard errors for the best models, according to AICc, per group, estimating the effect of body size on immature survival. Those groups in which the null is the best model are not included (see Table 1.8). The gradients are logistic regression slopes, calculated using SPLUS 2000 and are transformed according to Janzen and Stern (1998) so that they are comparable to selection gradients as proposed by Lande and Arnold (1983).

	gradient	*SE*	*LCL*	*UCL*
***Lestes congener* female, 1998**				
survival~Date				
Date	0.399	0.232	-0.055	0.854
survival~PC1+Date				
PC1	-0.416	0.298	-1.000	0.167
Date	0.582	0.277	0.038	1.126
survival~wing loading+Date				
wing loading	-0.429	0.320	-1.056	0.197
Date	0.565	0.271	0.033	1.097
***Lestes congener* male, 1998**				
survival~PC1+Date				
PC1	-0.889	0.376	-1.625	-0.153
Date	0.528	0.378	-0.212	1.269
***Sympetrum pallipes* male, 1999**				
survival~wing loading+wing loading^2+Date				
wing loading	9.449	3.247	3.085	15.812
wing loading^2	-9.185	3.174	-15.406	-2.964
Date	0.164	0.144	-0.119	0.446
survival~wing loading+wing loading^2+Date+wing loading:Date				
wing loading	11.224	4.394	2.612	19.835
wing loading^2	-10.676	0.515	-11.686	-9.666
Date	1.358	1.862	-2.290	5.007
wing loading:Date	-1.094	6.803	-14.427	12.239

Capture mark-recapture

Marking effect

No marking effect on survival was found in comparisons of CMR models (Table 1.10). Models with separate survival rates over the first interval following survival have roughly equivalent or slightly higher AICc values than those with constant survival over time.

Survival estimates

The best model typically estimated survival as constant over the season (Tables 1.11 to 1.13). When survival rates did vary over time, models that constrained survival to be a linear ($\Phi_{(linear)}$) or quadratic ($\Phi_{(linear+quadratic)}$) function of time or weather ($\Phi_{(weather)}$) often had better fit than $\Phi_{(t)}$, perhaps because they require fewer parameters. Recapture effort was included in the best model in only one group (*Lestes congener* female, 1998 – Table 1.11).

Table 1.10. Test of marking effect on survival. Models $\Phi_{(./a=1)}$ (in analyses with both teneral and mature groups) and $\Phi_{(a=1)}$ (mature only) estimate a different survival rate for mature individuals during the first interval following release while model $\Phi_{(.)}$ estimates constant survival over time.

Model	*Deviance*	*K*	*AICc*	*ΔAICc*	*AICc weight*
***Lestes congener* female 1998**					
$\Phi_{(.)}$, $p_{(t+effort)}$	378.16	3	384.25	0	0.73
$\Phi_{(./a=1)}$, $p_{(t+effort)}$	378.105	4	386.26	2.01	0.27
***Lestes congener* male 1998**					
$\Phi_{(./a=1)}$, $p_{(t)}$	726.98	11	749.74	0	0.56
$\Phi_{(.)}$, $p_{(t)}$	729.59	10	750.22	0.48	0.44
***Lestes disjunctus* male 1998**					
$\Phi_{(.)}$, $p_{(.)}$	527.58	2	531.62	0	0.61
$\Phi_{(a=1)}$, $p_{(.)}$	526.42	3	532.50	0.88	0.39
***Sympetrum pallipes* 1998**					
$\Phi_{(.)}$, $p_{(t)}$	840.72	10	861.22	0	0.70
$\Phi_{(./a=1)}$, $p_{(t)}$	840.35	11	862.95	1.73	0.30

Although teneral survival was poorly estimated, primarily due to low teneral recapture rates, there was some evidence to suggest that teneral survival was lower, especially in female *L. congener* and female *S. pallipes* (Figures 1.2, 1.3 – teneral survival is represented by the first interval). There was little conclusive evidence of a difference in daily survival rates between sexes (Table 1.14).

Table 1.11. Mark-recapture AIC results for models not including phenotype as a covariate for *Lestes congener*, 1998 and 1999, including -2log likelihood values (deviance). AICc values represent the fit of the model to the data, corrected for small sample sizes; lower values suggest a better fit. ΔAICc values show the distance in AICc units from the model with the lowest score. AICc weights represent the relative power of each model, given the current set of models and sum to 1 for all models included in the analysis. The cumulative AICc weights give an indication to the number of useful models. Only models with ΔAICc values up to ≥4.0 are included.

model	*K*	*deviance*	*AICc*	*ΔAICc*	*AICc weight*	*cumulative AICc weight*
***Lestes congener* female**						
1998						
$\Phi_{(a=1/.)}$, $p_{(effort)}$	3	377.68	383.77	0	0.21	0.21
$\Phi_{(a=1/linear)}$, $p_{(effort)}$	4	376.43	384.58	0.81	0.14	0.35
$\Phi_{(g)}$, $p_{(effort)}$	4	376.75	384.90	1.13	0.12	0.47
$\Phi_{(linear)}$, $p_{(effort)}$	4	377.28	385.43	1.66	0.09	0.56
$\Phi_{(g)}$, $p_{(g)}$	4	377.33	385.48	1.71	0.09	0.65
$\Phi_{(a=2/.)}$, $p_{(effort)}$	4	377.45	385.61	1.84	0.08	0.73
$\Phi_{(g)}$, $p_{(t)}$	10	365.18	386.05	2.27	0.07	0.80
$\Phi_{(weather)}$, $p_{(effort)}$	4	378.31	386.46	2.69	0.05	0.85
$\Phi_{(.)}$, $p_{(t)}$	9	368.06	386.77	3.00	0.05	0.90
$\Phi_{(linear+quadratic)}$, $p_{(effort)}$	5	376.80	387.03	3.26	0.04	0.94
$\Phi_{(.)}$, $p_{(.)}$	2	384.73	388.78	5.01	0.02	0.96
1999						
$\Phi_{(a=1/.)}$, $p_{(a=1/.)}$	4	84.75	93.37	0.00	0.33	0.33
$\Phi_{(a=1/.)}$, $p_{(.)}$	3	87.42	93.78	0.41	0.27	0.60
$\Phi_{(a=1/.)}$, $p_{(a=1/effort)}$	4	86.99	95.61	2.24	0.11	0.71
$\Phi_{(a=1/.)}$, $p_{(effort)}$	4	87.32	95.94	2.57	0.09	0.80
$\Phi_{(a=2/.)}$, $p_{(a=2/.)}$	4	87.35	95.97	2.60	0.09	0.89
$\Phi_{(a=2/.)}$, $p_{(.)}$	3	90.93	97.29	3.92	0.05	0.94
$\Phi_{(a=1/.)}$, $p_{(a=1/t)}$	12	70.17	99.64	6.27	0.01	0.95
***Lestes congener* male**						
1998						
$\Phi_{(t)}$, $p_{(a=1/t)}$	19	712.79	753.04	0	0.32	0.32
$\Phi_{(t)}$, $p_{(a=2/t)}$	19	713.10	753.35	0.31	0.28	0.60
$\Phi_{(t)}$, $p_{(t)}$	18	715.54	753.56	0.52	0.25	0.85
$\Phi_{(a=1/t)}$, $p_{(t)}$	19	716.20	756.44	3.41	0.06	0.91
$\Phi_{(a=1/t)}$, $p_{(a=1/t)}$	20	715.10	757.59	4.55	0.03	0.94
1999						
$\Phi_{(.)}$, $p_{(a=2/.)}$	3	157.05	163.36	0.00	0.50	0.50
$\Phi_{(a=2/.)}$, $p_{(a=2/.)}$	4	156.06	164.60	1.23	0.27	0.77
$\Phi_{(a=2/.)}$, $p_{(a=2/t)}$	10	144.28	167.47	4.10	0.06	0.83

The strongest support for mature survival selection on body size of mature adults was found in female *L. congener* in 1998, male *L. disjunctus* in 1998 and female *S. pallipes* in both years (Tables 1.15, 1.16). Selection on wing loading was relatively more common than selection on body size (PC1).

Table 1.12. Mark-recapture AIC results for models not including phenotype for *Lestes disjunctus* males and females, 1998, including -2log likelihood values (deviance). AICc values represent the fit of the model to the data, corrected for small sample sizes; lower values suggest a better fit. ΔAICc values show the distance in AICc units from the model with the lowest score. AICc weights represent the relative power of each model, given the current set of models and sum to 1 for all models included in the analysis. The cumulative AICc weights give an indication to the number of useful models. Only models with ΔAICc values up to ≥4.0 are included.

model	*K*	*deviance*	*AICc*	*ΔAICc*	*AICc weight*	*cumulative AICc weight*
***Lestes disjunctus* female, 1998**						
$\Phi_{(.)}$, $p_{(.)}$	2	87.42	91.52	0	0.36	0.36
$\Phi_{(weather)}$, $p_{(.)}$	3	86.46	92.65	1.13	0.20	0.56
$\Phi_{(linear)}$, $p_{(.)}$	3	87.38	93.57	2.05	0.13	0.69
$\Phi_{(weather)}$, $p_{(effort)}$	4	85.93	94.25	2.73	0.09	0.78
$\Phi_{(weather)}$, $p_{(linear)}$	4	85.95	94.27	2.76	0.09	0.87
$\Phi_{(linear)}$, $p_{(effort)}$	4	86.26	94.58	3.06	0.08	0.95
$\Phi_{(linear+quadratic)}$, $p_{(.)}$	4	87.25	95.57	4.05	0.05	1
***Lestes disjunctus* male, 1998**						
$\Phi_{(linear)}$, $p_{(.)}$	3	522.64	528.72	0	0.38	0.38
$\Phi_{(weather)}$, $p_{(.)}$	3	523.66	529.74	1.02	0.23	0.61
$\Phi_{(linear+quadratic)}$, $p_{(.)}$	4	522.21	530.34	1.62	0.17	0.78
$\Phi_{(.)}$, $p_{(.)}$	2	527.58	531.62	2.90	0.09	0.87
$\Phi_{(.)}$, $p_{(effort)}$	3	526.23	532.31	3.59	0.06	0.93
$\Phi_{(.)}$, $p_{(weather)}$	3	527.43	533.51	4.79	0.03	0.96

Lestes congener

Contrary to expectation, there was strong support for higher survival before rather than after maturity in female *L. congener.* The best models in both years included unique teneral survival parameters, indicating that separating teneral and mature survival improved the fit of the models (Table 1.11). The support is very strong in 1999 in which all models had a teneral survival difference, but slightly weaker in 1998 in which four models with a ΔAICc ≤4.0 have equal teneral and mature survival. The teneral survival estimate for 1998 is poor and effectively spans the range of zero to one (Figure 1.2). Model $\Phi_{(a=1/linear)}$, $p_{(effort)}$, however, has good support and estimates daily survival of tenerals to be 0.981±0.013 (95% CI= 0.927 - 0.995), and mature survival to decline from 0.977±0.013 in the first week after maturity to 0.924±0.029 in the last week.

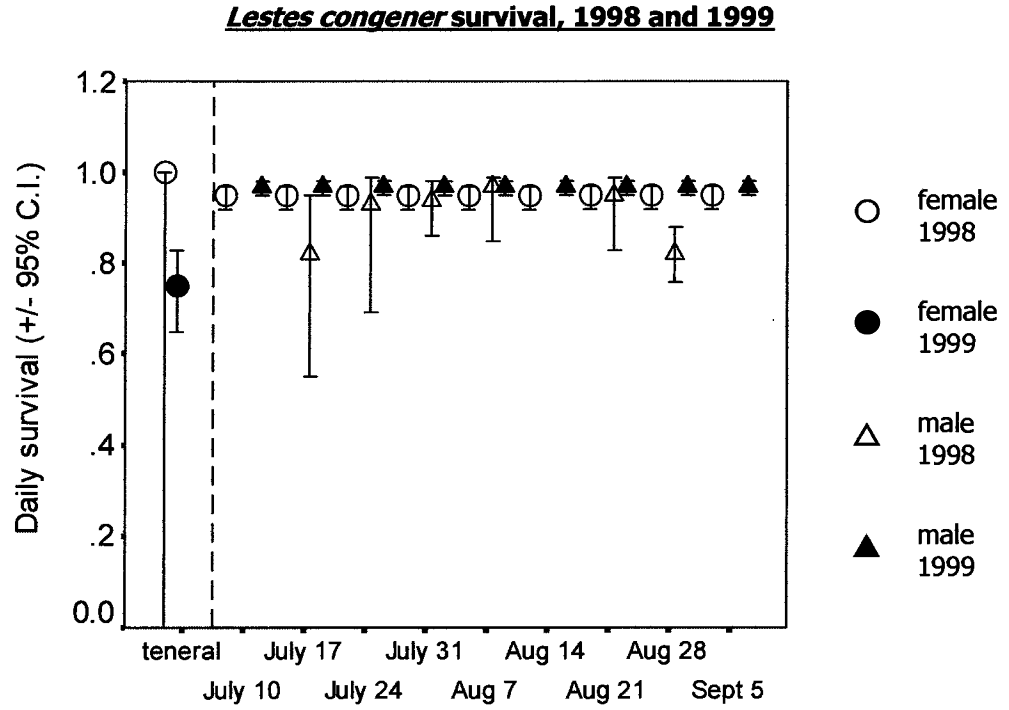
In contrast, teneral survival in 1999 was quite low, and mature survival was inestimable with the best models (Figure 1.2). The best model to simultaneously estimate teneral and mature survival in 1999 was $\Phi_{(a=1/.)}$, $p_{(a=1/t)}$ (ΔAICc=6.27), which specified a daily teneral survival rate of 0.799±0.077 (95% CI= 0.607 - 0.910) and a mature survival rate of 0.976±0.016 (95% CI= 0.913 - 0.944). When 1998 and 1999 data were combined, the best model indicated a difference in lifetime survival between those marked at emergence (Φ_1) and those marked after maturity (Φ_2) (Model $\Phi_{(g)}$, $p_{(g*t)}$ AICc=0: Φ_1= 0.968±0.013, 95% CI= 0.930 - 0.986; Φ_2= 0.922±0.019, 95% CI= 0.876 - 0.952), but there was no support for a difference between teneral and mature survival (Model $\Phi_{(a=1/.)}$, $p_{(g*t)}$ AICc=2.67: Φ_1= 1.000±0.249*E-07, 95% CI= 1.000 – 1.000; Φ_2= 0.947±0.011, 95% CI= 0.931 - 0.964). A likelihood ratio test could not be conducted because these models are not nested within each other.

Survival was affected by wing loading and date of capture in female *L. congener* in 1998; support is strong as the wing loading + date model has an AICc value nearly two units less than the next best model (Table 1.15). Individuals with smaller wing loading values and those initially captured later in the season had higher survival probabilities than others (Table 1.17). There was no indication of mature survival selection on body size in 1999; the null model had the greatest support; selection gradients were therefore not transformed.

Daily survival likely varied with time in male *L. congener* in 1998 (Table 1.11). Daily survival estimates ranged from 0.822 to 0.968 in the best model in 1998, with three parameters estimated as 1.0 (Figure 1.2). This was consistent among the three best models; re-running the models with these parameters set at 0.5 increased the deviance, confirming that they were not inestimable. The mean daily survival rate for teneral and mature combined was 0.945 when averaged over the season. The best estimate of teneral survival was 0.976±0.056 (95% CI= 0.265 – 0.999) from model $\Phi_{(a=1/t)}$, $p_{(t)}$ (ΔAICc=3.41).

Table 1.13. Mark-recapture AIC results for models not including phenotype for *Sympetrum pallipes*, 1998 and 1999, including -2log likelihood values (deviance). AICc values represent the fit of the model to the data, corrected for small sample sizes; lower values suggest a better fit. ΔAICc values show the distance in AICc units from the model with the lowest score. AICc weights represent the relative power of each model, given the current set of models and sum to 1 for all models included in the analysis. The cumulative AICc weights give an indication to the number of useful models. Only models with ΔAICc values up to ≥4.0 are included.

model	*K*	*deviance*	*AICc*	*ΔAICc*	*AICc weight*	*cumulative AICc weight*
***Sympetrum pallipes* female**						
1998						
$\Phi_{(\text{linear})}, p_{(.)}$	3	161.74	167.86	0	0.28	0.28
$\Phi_{(\text{weather})}, p_{(.)}$	3	161.74	167.86	0.01	0.28	0.56
$\Phi_{(\text{linear})}, p_{(\text{effort})}$	4	161.06	169.27	1.41	0.14	0.70
$\Phi_{(\text{weather})}, p_{(\text{effort})}$	4	161.10	169.30	1.45	0.14	0.83
$\Phi_{(\text{linear+quadratic})}, p_{(.)}$	4	161.65	169.85	1.99	0.10	0.94
$\Phi_{(.)}, p_{(.)}$	2	166.91	170.97	3.11	0.06	1
$\Phi_{(.)}, p_{(t)}$	9	157.85	176.80	8.94	0.00	1
1999						
$\Phi_{(\text{linear})}, p_{(a=2/\text{effort})}$	5	249.62	259.87	0.00	0.31	0.31
$\Phi_{(\text{linear})}, p_{(a=2/t)}$	12	235.09	260.44	0.57	0.23	0.54
$\Phi_{(a=1/\text{linear})}, p_{(a=2/\text{effort})}$	6	249.65	262.00	2.13	0.11	0.65
$\Phi_{(a=2/\text{linear})}, p_{(a=2/\text{effort})}$	6	249.83	262.19	2.32	0.10	0.75
$\Phi_{(a=1/\text{linear})}, p_{(a=2/t)}$	13	235.08	262.65	2.78	0.08	0.83
$\Phi_{(\text{linear+quadratic})}, p_{(a=2/t)}$	13	235.28	262.86	2.99	0.07	0.90
$\Phi_{(.)}, p_{(a=2/t)}$	11	240.96	264.09	4.22	0.04	0.93
***Sympetrum pallipes* male**						
1998						
$\Phi_{(t)}, p_{(.)}$	10	835.03	855.53	0.00	0.53	0.53
$\Phi_{(t)}, p_{(\text{effort})}$	11	833.33	855.92	0.39	0.44	0.97
$\Phi_{(.)}, p_{(t)}$	10	840.72	861.22	5.69	0.03	1
1998 ITEC						
$\Phi_{(t)}, p_{(m)}$	11	544.88	846.60	0	0.98	0.98
$\Phi_{(t)}, p_{(m/t)}$	18	538.79	855.47	8.88	0.01	0.99
1999						
$\Phi_{(t)}, p_{(a=1/t)}$	19	652.13	692.64	0.00	0.26	0.26
$\Phi_{(a=1/.)}, p_{(a=1/.)}$	4	684.76	692.89	0.25	0.23	0.50
$\Phi_{(.)}, p_{(a=1/t)}$	11	670.99	693.84	1.20	0.14	0.64
$\Phi_{(t)}, p_{(a=1/.)}$	11	672.72	695.57	2.93	0.06	0.70
$\Phi_{(g)}, p_{(a=1/t)}$	12	670.67	695.68	3.04	0.06	0.76
$\Phi_{(.)}, p_{(a=1/.)}$	3	689.78	695.85	3.21	0.05	0.81
$\Phi_{(a=1/.)}, p_{(a=1/t)}$	12	670.98	695.98	3.34	0.05	0.86
$\Phi_{(g)}, p_{(a=1/.)}$	4	688.34	696.47	3.83	0.04	0.90
$\Phi_{(a=1/t)}, p_{(a=1/t)}$	20	654.83	697.61	4.97	0.02	0.92
1999 ITEC						
$\Phi_{(.)}, p_{(t)}$	10	459.95	709.63	0	0.55	0.55
$\Phi_{(g)}, p_{(t)}$	11	459.89	711.71	2.08	0.19	0.74
$\Phi_{(.)}, p_{(g*t)}$	15	452.61	713.14	3.52	0.09	0.83
$\Phi_{(g)}, p_{(g*t)}$	16	450.66	713.40	3.78	0.08	0.91
$\Phi_{(t)}, p_{(g*t)}$	22	438.38	714.72	5.09	0.04	0.96



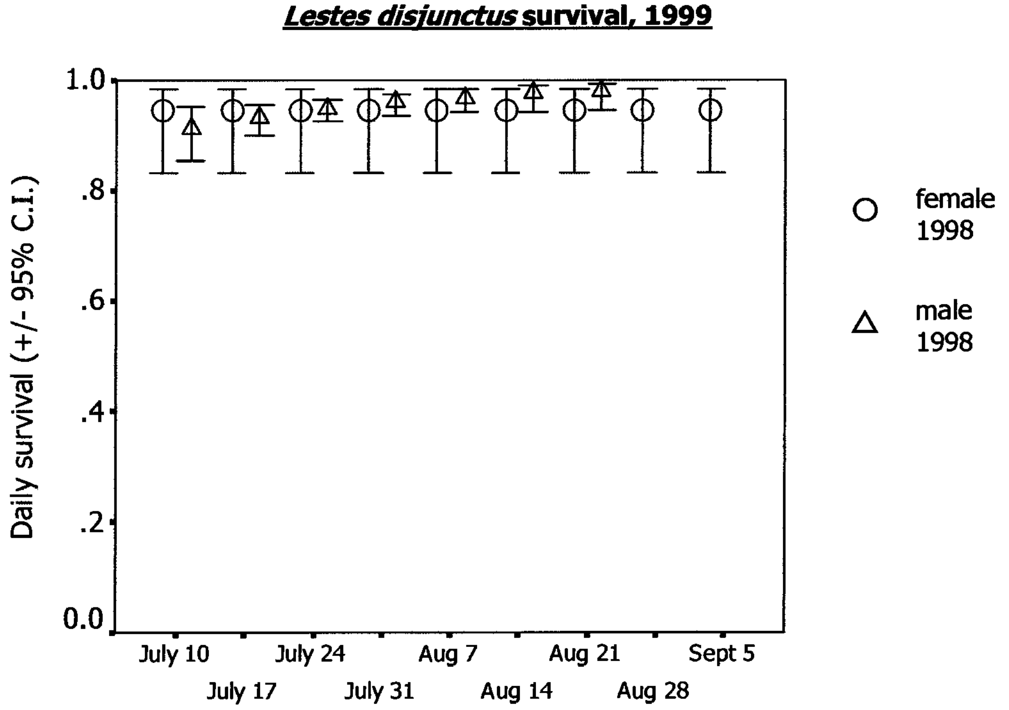
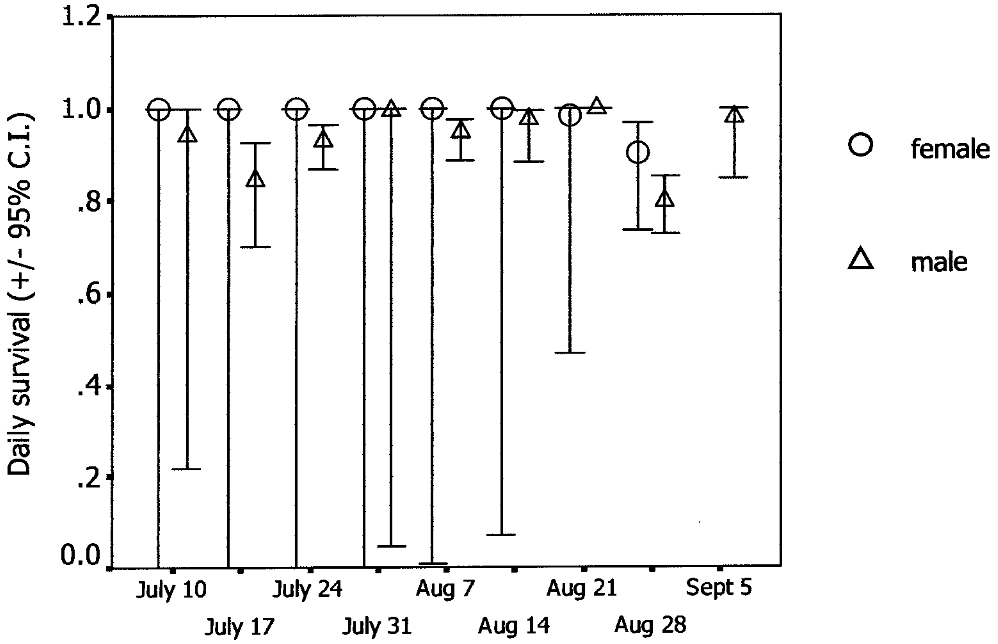


Figure 1.2. Estimated daily survival per week from best capture mark-recapture models including 95% confidence intervals for *Lestes congener* and *Lestes disjunctus.* The teneral values for female *L. congener* in both years represent survival over the season and are thus time-independent. All remaining intervals show daily survival for mature individuals per week interval. Estimates are from the models in each group with the lowest AICc values as shown in Tables 1.11 and 1.12.

***Sympetrum pallipes* daily survival, 1998**



***Sympetrum pallipes* daily survival, 1999**

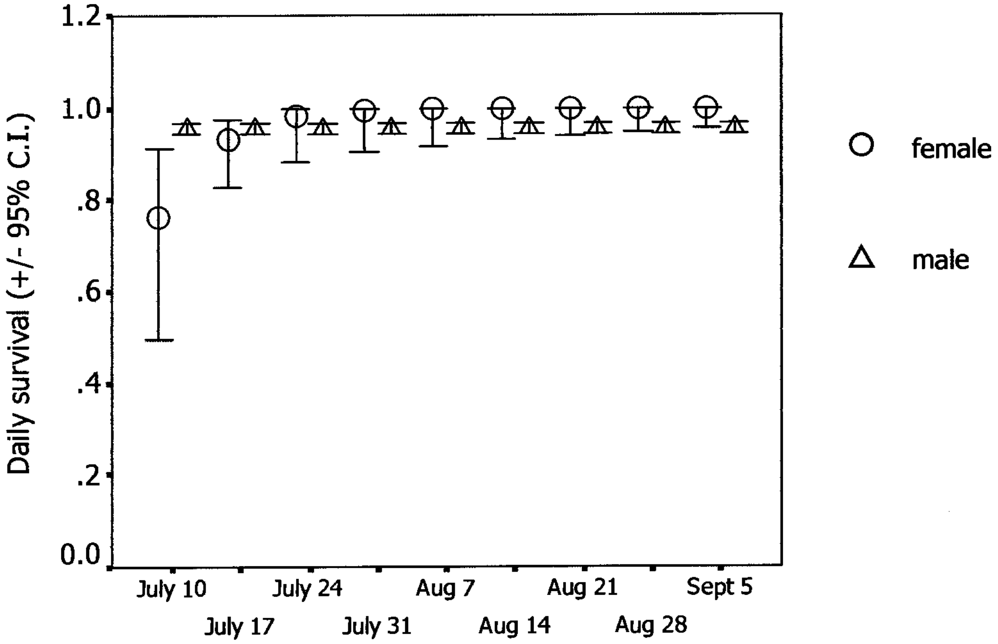


Figure 1.3. Daily survival estimates for mature individuals for each week interval from best capture mark-recapture models, including 95% confidence intervals for *Sympetrum pallipes*, 1998 and 1999. Estimates are from the models in each group with the lowest AICc values as shown in Table 1.13. Male estimates include only the immediate trap-dependence on capture models (ITEC - Pradel 1993).

Table 1.14. AICc results for comparison of survival rates between sexes in each species, 1998 and 1999. *K*= # parameters; deviance= -2log likelihood. Only those models with ΔAICc up to ≥4.0 are included.

Rank	***model***	***K***	***deviance***	***AICc***	***ΔAICc***	***AICc weight***	***cumulative AICc weight***
	Lestes congener						
	1998						
1	$\Phi_{(g)}$, $p_{(g*t)}$	20	325.95	1393.63	0	0.94	0.94
2	$\Phi_{(g*t)}$, $p_{(g*t)}$	36	296.33	1399.11	5.48	0.06	1.00
	1999						
1	$\Phi_{(.)}$, $p_{(g)}$	3	138.41	283.13	0	0.49	0.49
2	$\Phi_{(g)}$, $p_{(.)}$	3	140.04	284.76	1.63	0.22	0.71
3	$\Phi_{(g)}$, $p_{(g)}$	4	138.41	285.24	2.11	0.17	0.89
4	$\Phi_{(.)}$, $p_{(.)}$	2	143.41	286.04	2.92	0.11	1.00
	Lestes disjunctus						
	1998						
1	$\Phi_{(.)}$, $p_{(g)}$	3	106.61	621.16	0	0.58	0.58
2	$\Phi_{(g)}$, $p_{(g)}$	4	106.51	623.09	1.93	0.22	0.81
3	$\Phi_{(g)}$, $p_{(.)}$	3	110.31	624.86	3.70	0.09	0.90
4	$\Phi_{(t)}$, $p_{(g)}$	9	98.08	624.98	3.83	0.09	0.99
5	$\Phi_{(g)}$, $p_{(t)}$	9	101.94	628.85	7.69	0.01	1.00
	Sympetrum pallipes						
	1998						
1	$\Phi_{(t)}$, $p_{(g)}$	11	195.43	1071.56	0	0.96	0.96
2	$\Phi_{(g)}$, $p_{(g)}$	4	217.54	1079.31	7.75	0.02	0.98
	1999						
1	$\Phi_{(g)}$, $p_{(g*t)}$	20	170.15	982.02	0	0.78	0.78
2	$\Phi_{(.)}$, $p_{(g*t)}$	19	175.13	984.84	2.82	0.19	0.97
3	$\Phi_{(t)}$, $p_{(g*t)}$	26	163.97	988.89	6.88	0.03	1.00

In contrast, male *L. congener* survival was estimated as constant over the season in 1999 and equal for teneral and mature groups (0.969) in the best model (Table 1.11, Figure 1.2). The second and third best models specified unique teneral and mature survival and had some support (Table 1.11). Teneral survival estimates were lower in both models, but broadly overlapped mature estimates (e.g., $\Phi_{(a=2/.)}$, $p_{(a=2/.)}$: $\Phi_{teneral}$= 0.946±0.024, 95% CI= 0.874 – 0.978; Φ_{mature}= 0.981±0.013, 95% CI= 0.926 – 0.995).

There was strong support for a difference in survival between male and female *L. congener*. In 1998, model $\Phi_{(g)}$, $p_{(g*t)}$ had effectively exclusive support, but female survival was not estimable with this model (Φ_{male}= 0.947±0.007, 95% CI= 0.931 - 0.959). In fact, no models estimated female survival, suggesting that the improvement seen in models with $\Phi_{(g)}$ was merely because they did not have to simultaneously explain male and female deviance with the same parameter.

Table 1.15. AICc results for test of survival selection on body size for mature *Lestes congener*, 1998 and 1999, and *Lestes disjunctus*, 1998. *K*= # parameters; deviance= -2log likelihood. Only those models with ΔAICc up to ≥4.0 are included.

Rank	***model***	***K***	***deviance***	***AICc***	***ΔAICc***	***AICc weight***	***cumulative AICc weight***
	***Lestes congener* female**						
	1998						
1	wl+Date	6	368.08	380.41	0	0.39	0.39
2	PC1+PC1^2+Date	7	367.94	382.38	1.97	0.15	0.54
3	wl+wl^2+Date	7	368.04	382.48	2.07	0.14	0.67
4	wl+Date+wl*Date	7	368.42	382.86	2.46	0.11	0.79
5	PC1+PC1^2+Date+PC1*Date	8	366.73	383.30	2.89	0.09	0.88
6	wl+wl^2+Date+wl*Date	8	368.24	384.81	4.40	0.04	0.92
	1999						
1	Null	4	89.74	98.35	0	0.36	0.36
2	wl+Date	6	86.64	99.98	1.62	0.16	0.52
3	Date	5	89.28	100.22	1.87	0.14	0.66
4	wl+Date+wl*Date	7	85.15	100.96	2.61	0.10	0.76
5	PC1+Date	6	87.82	101.15	2.80	0.09	0.85
6	wl+wl^2+Date	7	86.64	102.45	4.10	0.05	0.89
	***Lestes congener* male**						
	1998						
1	wl+Date	11	740.88	763.65	0	0.27	0.27
2	PC1+Date	11	741.93	764.70	1.05	0.16	0.42
3	Date	10	744.53	765.16	1.52	0.12	0.55
4	wl+Date+wl*Date	12	740.75	765.65	2.01	0.10	0.65
5	wl+wl^2+Date	12	740.79	765.69	2.05	0.10	0.74
6	Null	10	745.17	765.80	2.16	0.09	0.83
7	PC1+PC1^2+Date	12	741.80	766.70	3.06	0.06	0.89
8	PC1+Date+PC1*Date	12	741.92	766.82	3.18	0.05	0.94
9	wl+wl^2+Date+wl*Date	13	740.52	767.58	3.94	0.04	0.98
10	PC1+PC1^2+Date+PC1*Date	13	741.77	768.83	5.18	0.02	1

Table 1.15 continued.

Rank	*model*	*K*	*deviance*	*AICc*	*ΔAICc*	*AICc weight*	*cumulative AICc weight*
	***Lestes congener*, male 1999**						
1	wl+Date	5	151.70	162.52	0	0.34	0.34
2	Null	3	157.05	163.36	0.85	0.22	0.56
3	wl+Date+wl*Date	6	151.59	164.74	2.22	0.11	0.67
4	wl+wl^{2}+Date	6	151.70	164.85	2.33	0.10	0.77
5	Date	4	156.97	165.50	2.99	0.08	0.85
6	PC1+Date	5	155.10	165.91	3.39	0.06	0.91
7	wl+wl^{2}+Date+wl*Date	7	151.40	166.96	4.44	0.04	0.94
	***Lestes disjunctus* female, 1998**						
1	Null	2	87.42	91.52	0	0.36	0.36
2	PC1+PC1^{2}+Date+PC1*Date	6	80.66	93.34	1.83	0.14	0.51
3	Date	3	87.42	93.61	2.09	0.13	0.63
4	PC1+PC1^{2}+Date	5	83.44	93.92	2.40	0.11	0.74
5	PC1+Date+PC1*Date	5	84.32	94.81	3.29	0.07	0.81
6	PC1+Date	4	86.84	95.16	3.64	0.06	0.87
7	wl+Date	4	86.90	95.22	3.70	0.06	0.93
8	wl+wl^{2}+Date	5	85.66	96.14	4.63	0.04	0.96
	***Lestes disjunctus* male, 1998**						
1	Date	3	518.00	524.08	0	0.21	0.21
2	wl+wl^{2}+Date	5	513.99	524.18	0.11	0.20	0.40
3	PC1+Date	4	516.54	524.67	0.60	0.15	0.55
4	wl+Date	4	516.79	524.92	0.84	0.14	0.69
5	wl+wl^{2}+Date+wl*Date	6	512.99	525.26	1.19	0.11	0.80
6	PC1+Date+PC1*Date	5	516.31	526.51	2.43	0.06	0.86
7	PC1+PC1^{2}+Date	5	516.46	526.65	2.58	0.06	0.92
8	wl+Date+wl*Date	5	516.63	526.83	2.75	0.05	0.97
9	PC1+PC1^{2}+Date+PC1*Date	6	516.29	528.57	4.49	0.02	1

I attempted additive models (i.e., $p_{(g+t)}$) because they require fewer parameters, but they provided no additional explanatory power. Running models with immediate trap dependence on capture (ITEC) improved the best model slightly but had no effect on model order. There was no apparent difference in survival between the sexes in 1999 (Table 1.14).

In male *L. congener* in 1998, positive directional mature survival selection on wing loading was indicated (Table 1.15, 1.17). Date was also included in the best model, but the resulting selection gradient was very small and the confidence interval overlapped zero (Table 1.17);

support for the effect of date on survival is thus weak. Model $\Phi_{(t)}$, $p_{(a=1/t)}$ was the best CMR model, but constraining this, or other time-dependent models, with individual covariates required the estimation of more parameters than the data could sustain; I therefore constrained model $\Phi_{(.)}$, $p_{(t)}$ (ΔAICc=12.77) because it was the best model that incorporated constant survival.

There was again support for selection on wing loading in male *L. congener* in 1999, but the margin of improvement of the wing loading+date model over the null was much smaller (Table 1.15). The wing loading selection gradients were again positive, indicating better survival for individuals with relatively larger wing loading values, but the confidence interval just overlaps zero, while the date gradient confidence interval broadly overlapped zero (Table 1.17).

Lestes disjunctus

Female *L. disjunctus* daily survival was estimated as constant over the season at 0.944 (Table 1.12, Figure 1.2). The confidence interval was fairly broad, probably due to relatively low recapture rates in this group (~0.05); however, the survival estimate was quite similar to that of female *L. congener* in the same year (Figure 1.2). Models with survival constrained as a linear effect of time and weather also had some support. Both model $\Phi_{(weather)}$, $p_{(.)}$ and $\Phi_{(linear)}$, $p_{(.)}$ estimate survival as declining over the season, but the former has a steeper slope (model $\Phi_{(weather)}$, $p_{(.)}$: Φ_1= 0.988, Φ_7= 0.856; model $\Phi_{(linear)}$, $p_{(.)}$: Φ_1= 0.954, Φ_7= 0.933). The beta parameters describing the slopes of these curves both overlap zero, however, suggesting the effect of time on survival is relatively weak.

In contrast, survival in male *L. disjunctus* was estimated as increasing over the season from 0.913 to 0.982 (Figure 1.2) in the best model, $\Phi_{(linear)}$, $p_{(.)}$ (Table 1.12). Support for the linear trend is strong in this group; the confidence interval of the beta parameter (that describes the slope of the curve) does not overlap zero (0.017 to 0.530). Additionally, there is a very narrow overlap in confidence intervals between Φ_1 and Φ_7 in this model (Figure 1.2). Model $\Phi_{(.)}$, $p_{(.)}$ (Table 1.12) has qualified support, but provides a relatively precise survival estimate (0.955±0.009, 95% CI= 0.934 – 0.969). Recapture probabilities averaged about 0.15 in this group.

There was no difference detected between survival estimates of male and female *L. disjunctus*; when both sexes were combined for mark-recapture analysis, the best model to fit the data had equal male – female survival (Table 1.14). Because survival estimate confidence intervals in female *L. disjunctus* were broad relative to males (Figure 1.2), a difference between the sexes would be difficult to find. Model $\Phi_{(g)}$, $p_{(g)}$ had some support at AICc weight= 0.22 and estimated female survival as lower than males, but confidence intervals broadly overlapped (Φ_{female}= 0.944±0.033, 95% CI= 0.831 - 0.983; Φ_{male}= 0.955±0.009, 95% CI= 0.934 - 0.969).

Table 1.16. AICc results for test of survival selection on body size for mature *Sympetrum pallipes*, 1998 and 1999. *K*= number of parameters; deviance= -2log likelihood. Only models with ΔAICc up to ≥4.0 are included.

Rank	*model*	*K*	*deviance*	*AICc*	*ΔAICc*	*AICc weight*	*cumulative AICc weight*
	***Sympetrum pallipes* female**						
	1998						
1	PC1+PC1^2+Date+PC1*Date	6	150.90	163.34	0	0.38	0.38
2	wl+wl^2+Date+wl*Date	6	151.88	164.31	0.97	0.23	0.62
3	wl+wl^2+Date	5	155.31	165.62	2.28	0.12	0.74
4	PC1+PC1^2+Date	5	155.61	165.92	2.58	0.10	0.84
5	PC1+Date	4	159.04	167.24	3.90	0.05	0.90
6	wl+Date	4	159.36	167.57	4.23	0.05	0.94
	1999						
1	wl+Date	9	229.61	248.37	0.00	0.33	0.33
2	Date	8	232.90	249.51	1.13	0.18	0.51
3	wl+Date+wl*Date	10	229.61	250.55	2.17	0.11	0.62
4	wl+wl^2+Date	10	229.61	250.55	2.17	0.11	0.73
5	PC1+Date+PC1*Date	10	230.21	251.15	2.77	0.08	0.81
6	PC1+Date	9	232.55	251.31	2.94	0.07	0.88
7	wl+wl^2+Date+wl*Date	11	229.07	252.20	3.83	0.05	0.93
8	PC1+PC1^2+Date	10	231.91	252.85	4.47	0.03	0.96
	***Sympetrum pallipes* male**						
	1998						
1	Date	11	836.54	859.14	0.00	0.29	0.29
2	wl+Date+wl*Date	13	833.41	860.24	1.10	0.17	0.46
3	PC1+Date	12	836.47	861.18	2.04	0.10	0.56
4	Null	10	840.72	861.22	2.08	0.10	0.66
5	wl+Date	12	836.53	861.23	2.10	0.10	0.76
6	PC1+PC1^2+Date+PC1*Date	14	832.98	861.94	2.80	0.07	0.83
7	PC1+PC1^2+Date	13	835.41	862.24	3.10	0.06	0.89
8	PC1+Date+PC1*Date	13	835.50	862.33	3.19	0.06	0.95
9	wl+wl^2+Date	13	836.28	863.11	3.97	0.04	0.99
10	wl+wl^2+Date+wl*Date	13	857.56	884.38	25.24	0	1
	1999						
1	Null	4	684.76	692.89	0.00	0.20	0.20
2	PC1+Date+PC1*Date	7	678.92	693.28	0.39	0.17	0.37
3	Date	5	683.35	693.54	0.65	0.15	0.52
4	PC1+PC1^2+Date	7	679.27	693.63	0.74	0.14	0.66
5	PC1+PC1^2+Date+PC1*Date	8	678.00	694.46	1.57	0.09	0.75
6	wl+Date	6	682.56	694.83	1.94	0.08	0.83
7	PC1+Date	6	682.59	694.86	1.97	0.08	0.90
8	wl+wl^2+Date+wl*Date	7	681.65	696.00	3.12	0.04	0.94
9	wl+wl^2+Date	7	682.00	696.36	3.47	0.04	0.98
10	wl+Date+wl*Date	7	682.56	696.91	4.03	0.03	1

There was no evidence of selection on body size in female *L. disjunctus* in 1998; the null model has over twice the support of the best constrained model (Table 1.15). In male *L. disjunctus*, two models had nearly identical support (Table 1.15). Both models indicate positive directional selection on date of capture, suggesting better survival later in the season, and the wing loading model indicates negative directional selection, as well as disruptive selection on wing loading, but the confidence intervals for both overlap zero (Table 1.17).

Sympetrum pallipes

Female *S. pallipes* survival was best modeled as a linear function of time or weather in both years (Table 1.13). Survival rates were effectively inestimable over the first half of the season in 1998, and only the last interval has a reasonably precise confidence interval (Figure 1.3); the trend in the last half of the season was for declining survival rates, although all estimates overlap. The mean daily survival rates over all intervals is 0.985, nearly equivalent to the estimate provided by $\Phi_{(.)}$, $p_{(.)}$ (ΔAICc= 3.11; Φ= 0.989±0.017, 95% CI= 0.798 - 1.000). I ran ITEC models, but they provided nearly identical results and thus are not presented here. Recapture rates were low in this group at ~0.03.

Female *S. pallipes* daily survival rate estimates and precision both increased over the season in 1999 (Figure 1.3). The best model, $\Phi_{(linear)}$, $p_{(a=2/effort)}$, provides an imprecise estimate of Φ_1 due to low recapture over this interval (3.8E-9); recapture estimates varied from 0.36 to 0.53 over the remaining intervals and thus precision was greater over these intervals. Since no mature individuals were released for the first five intervals, Φ_1 represents teneral survival for the first cohort released. The mean daily survival estimate over the season from this model is 0.961, but is 0.989 when the first interval is not included. The best model with constant survival over time, $\Phi_{(.)}$, $p_{(a=2/t)}$, estimated survival as 0.982±0.011 (95% CI=0.944 - 0.994), but had little support at ΔAICc=5.09. Given the similarity in survival estimates among models and years, there is strong support for a mean daily survival rate after maturity of about 0.982 to 0.989.

There was very strong support for selection on body size in female *S. pallipes* after maturity in both years (Table 1.16). However, beta parameters provided by MARK were either very large with large standard errors (i.e., >1000), or had standard errors of zero, and thus had no interpretive value.

Survival was estimated as varying over the season in male *S.* pallipes in 1998 but not 1999. In 1998, the two best CJS models both included time dependence and had a cumulative AICc weight of 0.97; ITEC models produced a similar result (Table 1.13). The best ITEC model estimated daily survival over all recapture occasions, but confidence intervals were wide, especially over the first interval (Figure 1.3). In this model, Φ_4, Φ_6 and Φ_7 are estimated as 1.0 with a very small standard error; re-running the model with these parameters fixed at 0.5 dramatically increased the model variance, thus confirming that they were estimable parameters. The ITEC model estimated slightly higher survival rates because it removed some of the bias associated with trap-dependence. When averaged over all intervals, the mean survival rate over the season is 0.943 for the best ITEC model (recapture = 0.278 following release, 0.138 for all following intervals) and 0.931 for the best CJS model (recapture = 0.265).

Time-dependent survival was again indicated in the best model in 1999 (Table 1.13). Estimates suggest greatest survival in the middle of the season with poorer survival early and late in the season, but confidence intervals are wide (Figure 1.3). In this model, mean daily survival rates over the season were 0.944. There is also strong support for a difference between teneral and mature survival; model $\Phi_{(a=1/.)}$, $p_{(a=1/.)}$ has almost equivalent support as $\Phi_{(t)}$, $p_{(a=1/t)}$ (Table 1.13), and provides teneral and mature survival estimates that do not overlap ($\Phi_{teneral}$= 0.915±0.021, 95% CI= 0.863 - 0.948; Φ_{mature}= 0.971±0.006, 95% CI= 0.955 - 0.981). The ITEC model did not support time-dependent survival, but provided a very precise estimate of overall survival for this group (0.957±0.006 - Figure 1.3). Recapture probabilities were effectively zero (~1E-15) over the first two recapture occasions for both model $\Phi_{(t)}$, $p_{(a=1/t)}$ and the ITEC model $\Phi_{(.)}$, $p_{(t)}$ because no individuals were recaptured over those intervals. Recapture probabilities for all subsequent intervals varied from 0.07 to 0.50 in the former model and 0.12 to 0.74 in the latter.

In male *S. pallipes* in 1998, date and possibly wing loading had an effect on mature survival probabilities (Tables 1.16, 1.17). The effect of date is not surprising because the best mark-recapture models specified time-dependent recapture rates in this group. No mature survival selection on body size was apparent in this group in 1999 (Table 1.16).

There was strong support for a difference in survival rates between the sexes in *S. pallipes* in 1998 but not 1999. In 1999, model $\Phi_{(g)}$, $p_{(g*t)}$, with separate male and female survival estimates, enjoyed large, but not quite exclusive support (Table 1.14). Models incorporating group effects were better than those with equal male and female survival, given a particular recapture structure (eg., $\Phi_{(g)}$, $p_{(t)}$, ΔAICc=34.13 < $\Phi_{(.)}$, $p_{(t)}$, ΔAICc=44.08; $\Phi_{(g)}$, $p_{(.)}$, ΔAICc=90.27

< $\Phi_{(.)}$, $p_{(.)}$, ΔAICc=102.89). In keeping with sex-specific model results from 1999, female survival was estimated as higher than male survival, although there was substantial overlap between the two (Φ_{female}= 0.988±0.013, 95% CI= 0.907 - 0.999; Φ_{male}= 0.957±0.006, 95% CI= 0.944 - 0.967). ITEC models did not improve estimates in this group.

Table 1.17. Transformed logistic regression survival selection gradients for mature individuals from best models (Tables 1.15, 1.16). Gradients are beta parameters provided by program MARK that estimate the effect of body size on survival and were transformed according to Janzen and Stern (1998) so that they are directly comparable to selection gradients, as proposed by Lande and Arnold (1983).

	estimate	*SE*	*LCL*	*UCL*
***Lestes congener*, female**				
1998				
survival~wing loading+Date				
wing loading	-0.0198	0.0081	-0.0040	-0.0356
Date	0.0058	0.0028	0.0004	0.0112
***Lestes congener*, male**				
1998				
survival~wing loading+Date				
wing loading	0.0101	0.0053	-0.0002	0.0205
Date	-0.0005	0.0068	-0.0137	0.0128
1999				
survival~wing loading+Date				
wing loading	0.0153	0.0085	-0.0013	0.0319
Date	0.0105	0.0104	-0.0099	0.0309
***Lestes disjunctus*, male**				
1998				
survival~Date				
Date	0.0318	0.0139	0.0047	0.0590
survival~wing loading+wing loading^2+Date				
wing loading	-0.2164	0.1690	-0.5477	0.1149
wing loading^2	0.2180	0.1655	-0.1063	0.5423
Date	0.0427	0.0188	0.0057	0.0796
***Sympetrum pallipes*, male**				
1998				
survival~Date				
Date	0.0194	0.0112	-0.0025	0.0413
survival~wing loading+wing loading:Date+Date				
wing loading	-0.0024	0.0018	-0.0059	0.0010
wing loading:Date	0.0345	0.0199	-0.0045	0.0734
Date	-0.0218	0.0164	-0.0540	0.0103

Discussion

Survival rates and selection on body size varied with sex and mating system. As expected, females gained more mass over the maturation period in every species and the difference between females and males was greatest in non-territorial species. Differences in survival appeared to broadly correlate with proportional mass gain over the maturation period, although teneral survival was difficult to estimate.

Body size changes between years

Unexpectedly, overall body size changed dramatically between years in all species: *Lestes* were bigger in 1999 than 1998 and *Sympetrum* were smaller. The differences were often greater than one standard deviation and were consistent between sexes. Size at emergence can be affected by larval density (Anholt 1990b; Banks and Thompson 1987b; Van Buskirk 1987, 1993), food supply (Anholt 1990a; Harvey and Corbet 1985; Johnson et al. 1985; Lawton et al. 1980; Plaistow and Siva-Jothy 1999), predation (McPeek 1997; McPeek and Peckarsky 1998; Stoks 2001a) and timing of emergence (Anholt 1990b; Baker et al. 1992; Banks and Thompson 1985b; Convey 1989; Fincke 1988; Gribbin and Thompson 1991b; Koenig and Albano 1987; Michiels and Dhondt 1989; Tsubaki and Ono 1987; Van Buskirk 1987).

In odonates, mass at emergence typically declines over the season (Anholt 1990b; Baker et al. 1992; Banks and Thompson 1985b; Convey 1989; Fincke 1988; Gribbin and Thompson 1991b; Koenig and Albano 1987; Michiels and Dhondt 1989; Tsubaki and Ono 1987; Van Buskirk 1987), with at least one exception (Rantala et al. 2001). This may be the result of an increase in size with a decrease in temperature (e.g., Hayashi 1990; Paulson 1966; Pickup and Thompson 1990), or a decrease in the amount of time available for development (Rowe and Ludwig 1991; Werner 1986; Werner and Anholt 1993; Werner and Gilliam 1984). Time-constrained larvae, i.e., those emerging late in the season, have been shown to develop faster at the expense of size at emergence (Johansson and Rowe 1999; Koenig and Albano 1987; Pickup and Thompson 1990; Plaistow and Siva-Jothy 1999).

Generational differences in body size of the magnitude seen here are not unusual (e.g., Michiels and Dhondt 1989). For example, Anholt (1991) found a decrease in mass at emergence of about 12.5% from one year to the next in male and female *Enallagma boreale*; however, both sexes emerged about 16 days later in the second year. In this study, there was no significant difference in the mean date of emergence in any group and emergence profiles were nearly identical between years. Thus, the timing of emergence could not account for size differences between years. The temperature over the emergence periods (estimated as 30 days from July 10 to August 8 of each year), however, was 2°C higher in 1998 (19.5°C) than 1999 (17.6°C – t=4.20; P= 0.0009). This is consistent with size differences seen in male and female *L. congener* and female *S. pallipes* at emergence. In contrast, male *S. pallipes* were larger at emergence in 1998, but the sample size was small (6) and included two outliers at 175 and 189mg (mean mass= 122mg with outliers; 92mg without). Larval density, food supply and predation may have also had an effect, but data on these measures were not collected.

If size is mainly the result of natural selection, then I would expect to detect selection acting in different directions in the two years. In female *L. congener*, I found no conclusive evidence of selection on body size prior to maturity and I found negative directional selection on wing loading in 1998 when adults were small. In males I found strong negative selection on body size before maturity and negative directional selection on wing loading following maturity. In male and female *S. pallipes*, I found little evidence of natural selection on body size either before or after maturity. Clearly, the realized heritability of these traits must be low and most of the annual variation in body size is due to environmental variation.

In most groups, the difference in body size between the years was larger at emergence than maturity. This suggests that selection is likely acting on body size during the immature stage to help maintain consistent mature body size over time. If this is true, then selection is not independent of size at emergence and the strength and direction of selection found in the field will vary between years, or episodes, relative to the available phenotype distribution.

Teneral survival

Odonates gain a large proportion of the resources needed for reproduction between emergence and sexual maturity (Anholt et al. 1991). While skeletal size is fixed at emergence, substantial mass gain occurs over this period in most species (see Anholt et al. 1991). In both sexes, mass gain consists of flight muscle tissue and fat reserves (Marden and Waage 1990), but males gain mostly thoracic mass while females gain abdominal mass, including egg clutches (Anholt et al. 1991; Marden 1989a). Mass gain comes at the expense of predator avoidance because animals must be active to forage; if this increases predation risk, survival should be lower in groups that gain relatively more mass.

Teneral survival was only estimable in three groups, but there was strong support to suggest that teneral survival was lower than mature survival. In female *L. congener* and *S. pallipes*, daily survival over the maturation period was estimated as 0.750 and 0.762, respectively. Confidence intervals were relatively wide, but upper confidence limits for both were less than any estimate of post mature survival. In male *S. pallipes*, the best model estimated no difference between teneral and mature survival, but the second-best model had nearly identical support and estimated teneral survival (0.915) as lower than mature survival (0.971) with confidence intervals that do not overlap. Female *L. congener* and *S. pallipes* had the lowest teneral survival while male *S. pallipes* had the next lowest survival, and male *L. congener* had teneral survival that was not detectably different from mature survival. These results agree well with predictions.

Females have lower survival than males over sexual maturation in at least four damselflies (Anholt 1991; Bick and Bick 1961; Garrison 1978; Hamilton and Montgomerie 1989), and one libellulid dragonfly (Koenig and Albano 1987). For example, female *Enallagma hageni* were recaptured in lower proportions than males after release at emergence in two successive years and sex ratios were female-biased, leading the author to conclude that survival over the maturation period was lower for females than males (Fincke 1982). In *Ischnura elegans*, recapture and survival estimates incorrectly predicted sex ratios in mature populations, suggesting that males have a lower survival rate than females in *I. elegans* over the maturation period (Anholt et al. 2001). The same study, however, found no such difference in *Coenagrion puella*. In the zygopteran *Pyrrhosoma nymphula*, females did not have significantly different daily survival rates over sexual maturation, but took 6 days longer to mature, leading to lower survivorship over this period (Bennett and Mill 1995).

Differences in survival between males and females over the maturation period appear to reflect the greater proportional mass gain females experience over this period. The additional mass gain in females is necessary for the production of egg clutches and likely increases potential fecundity. In at least 68 species of insects, female body size has been found to be a principal constraint on potential fecundity (Honek 1993). Food intake is necessary for mass gain and has also been shown to be strongly correlated with the number of eggs in the abdomen of female *Ishnura verticalis* (Richardson and Baker 1997). The trade-off between mass gain and survival, however, appears to put females at greater risk of predation because survival is lower than in males.

Teneral survival selection

Females

As expected, females gained at least twice the mass of males over the maturation period and the difference was greater in non-territorial species than territorial species. Relatively weak negative directional selection was found in female *L. congener* in 1998 and none was found in 1999. Further, selection gradients were weaker than in male *L. congener* in which there was strong negative selection on body size over the maturation period in 1998, but none detected in 1999.

The opportunity for selection was greater in females than males because of larger variance in body size measures (Table 1.5). If mass gain is tied to predation risk and proportional to size at emergence, then selection on body size should have been stronger in females than males, but the difference should have been smaller in *L. congener* than *S. pallipes*. However, since females have no eggs at emergence, additional mass gain need not be related to initial body size, and mass gained could all go to reproduction. Thus, selection on body size in females over the maturation period should be neutral unless mass gain is proportional to size at emergence. Of the groups with adequate sample sizes of individuals weighed at emergence and after maturity, mass gain in female *L. congener* was correlated with initial size (PC1 at emergence), but weaker in other groups (female *L. congener*, 1999: r= 0.672, n= 5, P= 0.380; male *L. congener*, 1999: r= -0.199, n= 14, P= 0.496; female *S. pallipes*, 1999: r= 0.104, n= 19, P= 0.673; male *S. pallipes*, 1999: r= 0.228, n=38, P= 0.169).

If selection on body size in females was strong and directional, sample sizes should have been adequate to detect it (Table 1.1). It is possible that either there was no pre-maturity selection on body size in females or there was non-random emigration that obscured selection in these groups. For example, if larger individuals are more likely to survive, but also more likely to disperse, little difference would be seen in the frequency distribution of those seen again with those never seen again. The opportunity for selection on body size was strongest in female *S. pallipes*; however, I was not able to detect natural selection in this group. Weak selection would be difficult to detect due to a low proportion of recaptured tenerals in this group (Table 1.1).

Males

The strongest evidence for selection over the maturation period was in male *S. pallipes* in 1999, which suggested strong positive linear selection on wing loading with equally strong stabilizing selection. Wing loading can be seen as a surrogate for energy reserves or flight muscle proportions relative to body size. Those individuals with very high, and especially very low, wing loading values survived the maturation period less well. Very high wing loading values have the potential to affect the maneuverability of an individual as the wings become over-loaded while very low wing loading values suggest a lack of energy reserves or flight muscle power leading to a decrease in survival. Further, small males may have to forage more frequently than large males due to lower reserves. This could result in selection against small males.

The direction of selection was also inconsistent with expectations because *Lestes* were smaller in 1998 than 1999; if a long-term optimum body size exists, selection should have been positive in 1998 or possibly negative in 1999. These results suggest that either selection is stronger during another life stage, for example during larval stages, or that absolute body size is much less important than body size relative to other members of the cohort. Further, stochastic conditions such as weather and the density of predators, prey and conspecifics may have a larger effect on survival than body size.

In male *Enallagma boreale*, natural selection on body size was found to alternate between years (Anholt 1991): in the first year larger males survived to maturity while in the second, smaller males survived, although the difference was not significant; concurrently, there may have been stabilizing selection on body size in females in the first year, but none found in the second. These results underscore the fact that selection is context-specific and as conditions change between years and selection events, the nature of selection itself is also likely to change.

Survival of mature individuals

The factors affecting survival and natural selection change after maturity. Females only return to the pond to mate and oviposit; the remainder of the time they are away from the pond foraging to facilitate egg production. Females lose substantial mass at oviposition, in some cases up to 20% of their body mass (pers. obs.), and must therefore actively forage to replenish their complement of eggs. Males spend much of their time at the pond attempting to mate and may be at a higher risk of predation due to a high density of individuals at the pond, which attracts predators. Frogs, birds, spiders, as well as other odonate species are found in large numbers at the pond and present a high degree of risk to courting males (Corbet 1999). However, females occupy different habitats than males after maturity; this complicates conclusions that foraging activity levels have an effect on mature survival. While females do gain and lose more mass than males, and must therefore capture more or larger prey, they are exposed to a different complement of predators while away from the pond. Further, females are subject to little, if any, intrasexual competition for matings because most females mate (Corbet 1999). In comparison, male-male competition for matings can be intense in many species (e.g., Banks and Thompson 1985b; Grether 1996a; Koenig and Albano 1985; Moore 1990; Tsubaki and Ono 1987; Van Buskirk 1987). Thus, resources in males may be diverted from maintenance of survival to intrasexual competition for matings, further obscuring the relationship between foraging activity and survival.

All else being equal, since energy, and therefore mass, is more important to females than males, we would expect females to have lower daily survival rate than males. In both *Lestes* species, however, male and female daily survival rates after maturity were similar. Mature female *L. congener* daily survival rates were 0.954 (1998; not inestimable in 1999), compared to 0.945 (1998) to 0.969 (1999) in male *L.* congener. Female *L. disjunctus* survival rates were 0.944 (1998), while male rates varied from 0.913 to 0.982 (1998; mean= 0.954). Female *S. pallipes* survival rates were somewhat higher than males at approximately 0.985 (1998 and 1999) as compared to 0.943 (1998) to 0.957 (best model, 1999) and 0.971 (second-best model, 1999) in males. There was substantial uncertainty in female survival rates, however, especially in 1998, and confidence intervals overlap for every interval in both years (Figure 1.2). Moreover, when male and female recapture histories were combined for each species, there were no convincing differences found between sexes. The lack of a detectible difference may simply reflect methodology; given relatively low recapture rates for females, large sample sizes are necessary to precisely measure daily survival in females.

Odonates display a wide range of behavioral and demographic characteristics; thus any differences in survival between sexes are expected to be highly variable among species. For example, while most species mate repeatedly, females of *Ischnura elegans* mate only once, thus the mortality risk associated with mating is reduced in this species. While the following studies did not employ mark-recapture techniques, several found lower mature survival in females than males (Banks and Thompson 1985a; Bennett and Mill 1995; e.g., Bick and Bick 1961; Koenig and Albano 1987) while others found higher female survival (Robinson et al. 1983) or no measurable difference (e.g., Andres and Rivera 2001; Hafernik and Garrison 1986; Hamilton and Montgomerie 1989). In a concurrent mark-recapture study of two damselfly species, female survival was lower (0.579) than male (0.812) in *Ischnura elegans*, but no such difference was found in *Coenagrion puella* (Anholt et al. 2001).

Survival selection after maturity

Females

After maturity, I found negative directional selection on wing loading in female *L. congener* in 1998, but none in 1999, and positive directional selection on wing loading in both years in male *L. congener*. I found no selection in female *L. disjunctus* and survival in male *L. disjunctus* was mainly a function of date, not body size. In both *Lestes* species in both years, models including wing loading had better fit than those with PC1, with the exception of female *L. disjunctus* in 1998, in which case the null model had the greatest support. Logistic regression results provided strong support for natural selection in female *S. pallipes*, but selection gradients were not interpretable. There was also some support for negative selection on wing loading in mature male *S. pallipes*, but confidence intervals overlapped zero by about 8%.

Body size, including wing or abdomen length or mass, has been used as a predictor of fitness in several studies of natural selection in odonates (e.g., Andres and Rivera 2001; Anholt 1991; Banks and Thompson 1987a; Fincke 1986, 1988; Grether 1996b; Michiels and Dhondt 1989). Several have shown a significant positive correlation between large size and components of fitness (Banks and Thompson 1985b, 1987a; Cordero 1995; Fincke 1992; Harvey and Corbet 1985; Harvey and Walsh 1993; Koenig and Albano 1985; Tsubaki and Ono 1987), while others have shown weak or no effect (Anholt 1991; Fincke 1986, 1988; Koenig and Albano 1987; Richardson and Baker 1997; Van Buskirk 1987).

Few studies have examined natural selection on body size in female odonates. No relation was found between abdomen length and the number of days present at a pond (local survival) in female *Sympetrum danae* (Michiels and Dhondt 1989). Longevity in lab-reared female *Ischnura graelsii* (Cordero 1991) was correlated with large size; similar results were found in female *Enallagma ebrium*, but individuals were captured at emergence, then allowed to starve in the lab (Leung and Forbes 1997). None of these studies have estimated survival in the wild while taking into account variation in recapture probabilities. However, 68% of the total opportunity for selection in females of the dragonfly *Erythemis simplicicollis* (McVey 1988) and 23-34% in females of the damselfly *Enallagma hageni* (Fincke 1986) was associated with longevity, and an estimated 70% of lifetime egg production is explained by reproductive lifespan in *Coenagrion puella* (Banks and Thompson 1987a). Thus, assuming these estimates are not biased by variation in recapture rate, longevity (or survival) is an important component of lifetime reproductive success.

In this study, I detected selection for lower wing loading in female *L. congener* in 1998, but not in 1999, and I found no selection on female *L. disjunctus.* There was strong support for selection in female *S. pallipes,* but selection gradients were inestimable due to heterogeneity in survival and recapture parameters. Since wing length is fixed at emergence, but mass is variable throughout the season, wing loading can be seen as a time-variable trait. Mean mass was recorded for females that were weighed more than once, but most were weighed only once; thus wing loading values recorded are for the time of capture but likely vary throughout the season. Mass in females is affected by fat and flight muscle levels (Marden and Rollins 1994; Marden and Waage 1990), as well as clutch size (Banks and Thompson 1987a; Thompson 1990). Since it was not known if females were captured before or after oviposition, it is not possible to determine which ones were carrying a full clutch. Thus, it is possible that apparent selection on wing loading is a reflection of the presence or absence of a complete complement of eggs. If this were the case, then those that had not yet oviposited had a lower probability of survival than those that had. This would support the premise that mating and ovipositing is dangerous. Alternatively, if fat or flight muscle levels are responsible for variation in wing loading values, then those individuals with higher fat or muscle content were less likely to survive. Increased fat reserves (or clutch mass) may decrease maneuverability and put an animal at greater risk of predation. There may be also be a trade-off between the ratio of flight muscle to mass and fat reserves, as found in male *Plathemis lydia* (Marden 1989a), so that increased maneuverability comes at the cost of a decreased nutritional state.

Males

Longevity should be a relatively more important component of lifetime reproductive success in non-territorial than territorial species. If longevity is correlated with phenotype, then selection should be easier to measure in male *L. congener* than male *S.* pallipes. As predicted, there was better evidence of selection in male *Lestes* than in *S. pallipes* in both years. Positive directional selection on wing loading was found in male *L. congener* in similar strengths in both years, in spite of the fact that body size was much larger in 1999. Results were not consistent between *Lestes* species: male *L. disjunctus* survived better later in the year, but there was little support for selection on body size. In male *S. pallipes,* there was evidence of negative directional selection on wing loading in 1998, but transformed selection gradients overlapped zero, and there was no evidence of survival selection on body size in 1999.

Overall body size, as represented by PC1, is a relatively stable measure over the season because two of the three measures (abdomen and wing length) used reflect skeletal size, which is fixed at emergence, while only mass varies throughout the season. Since wing loading can be seen an estimate of energy levels or reserves, it would appear that male *L. congener* with larger energy reserves survived better than others in both years.

These results are at variance with findings from other studies. Sokolovska et al. (2000), in a meta-analysis of the effect of body size on fitness, found that the mean effect size of the correlation between longevity and body size was much larger in males of territorial ($z(r)$= 0.27, P= 0.004, n= 3) than males of non-territorial species ($z(r)$= 0.047, P= 0.022, n= 7). Thus, they concluded that longevity was a function of body size for males of both mating systems and that the relationship was stronger in territorial species. However, their *a priori* hypothesis did not include linear selection for small size or stabilizing selection and the study may have included some inappropriate data (Thompson and Fincke 2002). In studies that do address these issues, the data are too few to be conclusive. Stabilizing natural selection was found on mass in male *Coenagrion puella*, and longevity was found to be a major determinant of lifetime mating success (Banks and Thompson 1985b). Earlier emerging male *Sympetrum danae*, a non-territorial dragonfly, had longer abdomens and correspondingly greater longevity than smaller conspecifics (Michiels and Dhondt 1989) and in *Lestes sponsa*, also non-territorial, males with intermediate-sized abdomens appeared to have greater longevity, but the results were non-significant (Stoks 2000). No studies are known that have investigated the role of body size in survival in territorial odonates. While the data from this study indicate that body size is important in longevity, and thus lifetime reproductive success, especially in males of non-territorial species, more studies are needed to determine if this is a consistent pattern among odonates.

Linear vs. stabilizing selection

Within episodes, stabilizing selection was indicated as the most likely form of selection on body size. Cubic spline selection curves for selection on overall body size (PC1) before maturity (Figure 1.1) typically showed decreasing fitness in the tails of the distribution; where they did not, confidence intervals were too wide to support definitive conclusions. In comparison, selection curves for wing loading were usually directional, with the exception of male *S. pallipes* in 1999. This is the only group in which selection was strongly supported by logistic regression; results showed that there was both a strong directional and stabilizing gradient in this group. In all other groups, AIC results chose the null or linear model, but transformed selection gradients all overlapped zero to some degree.

Analysis of survival selection after maturity gave strongest support to linear models of selection on wing loading or date (Tables 1.15 – 1.17). Specifically, survival was shown to be a decreasing function of wing loading in female *L. congener* in 1998, and an increasing function in male *L. congener* in both years. It is possible that the form of selection is too complex to be estimated using a simple linear or quadratic expression;, however more complex models were not constructed because they had not been included in any *a priori* hypotheses. Further, tests of stabilizing selection require larger sample sizes, because of the increased number of parameters, which were available for some groups but not others.

There were no groups in which selection on a trait was in opposing directions before and after maturity. Male *L. congener* with small body sizes at emergence were more likely to survive up to maturity in 1998, and those with large wing loading values were more likely to survive after maturity in both years. However, small individuals with large wing loading values appeared to be just as likely to survive as large individuals with large wing loading values, although this was not directly tested.

The methodology employed in this study proved to be effective at measuring selection, but cubic spline fitness curves often strongly suggested selection that was not corroborated by logistic regression. It may be that either sample sizes were too small or fitness functions were too complex to be described by simple regression models. In the former case, sample sizes, especially of tenerals, could be increased to get a more precise measurement of selection; in the latter, it is difficult to construct models with multiple modes and dips that make biological sense and interpretation of results of third or fourth order polynomial equations would be difficult to interpret and have little biological value.

Lifetime reproductive success is most accurately measured as the number of offspring produced by an individual, but this has rarely been done in an odonate species (e.g., Fincke and Hadrys 2001). A profitable methodology would be to use DNA techniques to measure offspring production of individuals and test for the importance of body size as a predictor of lifetime reproductive success. Concurrently, survival could be estimated over the immature and mature period using mark-recapture methods as employed here, and mating success could be estimated as described in Chapter 2. This would allow a definitive measure of the importance of body size in determining fitness during the four main selective episodes in the odonate life-cycle: larval survival, immature adult survival, mature adult survival and mating success. Given changes in body size, type and direction of selection and environmental conditions between years, this methodology would give a much more comprehensive picture of selection on odonates if it were conducted on at least two successive generations.

CHAPTER 2

PHENOTYPIC SEXUAL SELECTION SHAPED BY MATING SYSTEM IN MALES OF TWO NON-TERRITORIAL DAMSELFLIES AND A TERRITORIAL DRAGONFLY

Introduction

The number of viable mature offspring produced by an individual defines its darwinian fitness, but can be almost impossible to measure in the field. Components of male lifetime reproductive success are longevity, mating frequency, mate fertility and parental genetic quality (Brown 1988). Mating success or frequency is often the easiest of these to measure in the field, and selection on mating success may be, on average, stronger than selection on survival in nature (Kingsolver et al. 2001).

Components of fitness can be strongly affected by body size (mammals: Clutton-Brock 1989; birds: Price and Grant 1984; insects: Thornhill and Alcock 1983). In insects, large size (Blackmore and Lord 2000; Blanckenhorn et al. 2002; Honek 1993; Lauziere et al. 2000; Lefranc and Bundgaard 2000; Logan et al. 2001; Partridge 1988; Peckarsky et al. 1993; Preziosi et al. 1996; Sopow and Quiring 1998) and food intake (Blanckenhorn et al. 1995; Richardson and Baker 1997) can increase fecundity in females, and increase male mating success (Conrad and Pritchard 1992; Cordero 1995; Fairbairn and Preziosi 1996; Harvey and Walsh 1993; Michiels and Dhondt 1991; Rivera et al. 2002) and territorial success (Fincke 1982, 1984, 1992; Moore 1990).

Odonata, including Suborders Anisoptera (dragonflies) and Zygoptera (damselflies), displays a large variation in mating behaviour, even among morphologically similar species (Corbet 1999), and is therefore a useful taxon in which to study the relationship between mating behaviour and phenotype. Odonates are large and relatively easy to observe and handle and one can observe the entire reproductive lifespan of an individual in one flying season. Due to these amenable characteristics, odonates have been the subject of several studies of natural and sexual selection (Andres et al. 2000; Anholt 1991; Cordero 1995; Fincke 1986; Grether 1996b; Harvey and Walsh

1993; Kasuya et al. 1997a; Koenig and Albano 1987; McVey 1988; Michiels and Dhondt 1991; Moore 1990; Stoks 2000).

Odonate mating systems have generally been classified by the degree to which one sex can control access to copulations or other necessary resources (Campanella 1975; Conrad and Pritchard 1992; Corbet 1980; Fincke 1997; Waage 1984b). The presence or absence of territoriality is of primary importance in describing these systems (Conrad and Pritchard 1992; Emlen and Oring 1977). Odonate operational sex ratios are usually highly male-biased; females are consequently a limiting resource (Corbet 1999). Mating is energetically costly (Rowe 1994; Thornhill and Alcock 1983; Watson et al. 1998) and increases the potential of predation (Magnhagen 1991; Michiels and Dhondt 1990; Rehfeldt 1992b) and harassment by males. Females can fertilize several clutches of eggs with the sperm from one copulation (Corbet 1999) and therefore avoid the rendezvous site when possible. As a result, male intrasexual competition for mating opportunities can be intense. Physiological and behavioural adaptations such as sperm competition, mate guarding and territoriality have evolved as a consequence of this intrasexual struggle.

The Ghiselin-Reiss small-male hypothesis (Ghiselin 1974) argues that sexual size dimorphism (SSD) with larger females should evolve in species exhibiting scramble competition because small males can devote more time to reproduction than foraging and therefore increase their lifetime reproductive success. Alternatively, in species with male-male territorial competition, large size should play a more important role in determining mating success, resulting in a reduced level of SSD relative to non-territorial species. If the above holds true, then we would also expect to see weaker selection on male body size in non-territorial species.

Males of non-territorial odonates do not control oviposition sites; they converge at the rendezvous site and engage in scramble competition for females (Corbet 1999). Direct male-male competition is weak and male mating success is thought to be determined mainly by chance. Other aspects of lifetime reproductive success, such as longevity, and the number of days at the rendezvous site should therefore be more important. If foraging is risky, or takes time away from mating, we would expect non-territorial males to forage only when necessary to maintain survival and reproductive potential. Since large size should not benefit males that engage in scramble competition, selection on body size should be relatively weaker and less likely than in territorial species. Indeed, where agility is advantageous, we might expect smaller males to have higher success (Crompton et al. 2003; Neems et al. 1992, 1998).

Alternatively, males of territorial odonates attempt to control resources necessary for reproduction, typically by establishing and defending suitable oviposition sites needed by females. Males must compete directly with each other to establish and maintain territories, and therefore win access to copulation opportunities with females. Within a territorial species, alternative mate-acquiring strategies exist (Forsyth and Montgomerie 1987). Males may attempt to encounter females away from the meeting site or may attempt to copulate with females that are not defended by territorial males, but territorial males usually realize greater mating success (Fincke 1992; Ito 1960; Plaistow and Siva-Jothy 1996; Tsubaki and Ono 1987). Further, most odonates are capable of removing competitor's sperm when copulating with a female (Waage 1984b, 1986). This gives territorial males a further advantage because females that copulate with them in order to get access to their territories are certain to be using their sperm and not those of a competitor. Thus, if territorial males are able to control all, or most, of the females in their territories, then alternative mating tactics are unlikely to be successful.

Most territorial disputes are won by the resident and do not turn into escalated bouts, except when there is confusion over the owner of the territory (Waage 1988). However, large size appears to be important in territorial males. Territorial males are often larger than satellite males (Fincke 1984, 1992; Marden and Waage 1990; Moore 1990; Plaistow and Siva-Jothy 1996), and they often have much higher mating success both in terms of the number of copulations and the number of eggs fertilized per copulation (Fincke 1992; Ito 1960; Miller 1983; Plaistow and Siva-Jothy 1996; Tsubaki and Ono 1987). Most of the mass change in mature male odonates occurs in flight muscle tissue and fat, both of which can confer greater mating success in territorial males (Marden 1994; Marden and Rollins 1994; Marden and Waage 1990). Flight muscle tissue is important for manoeuvrability and should help the territory holder guard his territory and his mates; fat reserves allow an individual to forgo foraging for longer periods of time and to stay on the wing longer, which can be crucial in escalated disputes (Marden and Waage 1990; Plaistow and Siva-Jothy 1996).

Yet large size has energy demands that may incur costs, possibly leading to a fundamental trade-off between growth and survival (Peckarsky et al. 2001; Werner and Gilliam 1984), where more active animals are at higher risk of predation (Abrahams and Dill 1989; Clutton-Brock 1989; Kohler and McPeek 1989; Magnhagen 1991; Peckarsky et al. 1993; Peckarsky et al. 2001; Rehfeldt 1992a). Large size may consequently have inescapable negative consequences. Since territorial males usually realize greater lifetime reproductive success than those that adopt alternative strategies (see above), one can assume that the benefits of territoriality for large individuals outweigh the consequences. I therefore expect that sexual selection should favour large males in territorial species, although this must have limits relative to the effect of size on survival.

The form of male intrasexual competition may have an effect on sexual size dimorphism. Female body size affects potential fecundity in many species of insects (Honek 1993). In odonates, the number of eggs in the abdomen of the female damselfly, *Ischnura verticalis*, was strongly correlated with both short and long term food intake (Richardson and Baker 1997). These benefits are not realized in males because sperm production is less energetically costly than egg production (Bateman 1948; Trivers 1972). If selection favours large females in general and large males in territorial, but not non-territorial species, we would expect sexual size dimorphism to be greater in non-territorial than territorial species (Anholt et al. 1991).

Selection can be intrasexual, as in competition among males for access to females, or intersexual, (epigamic) such as in female choice for desirable male attributes (Bateman 1948). Female mate choice is expected to occur when females can judge mates of superior genetic quality or those that can provide material benefits to increase their reproductive success (Thornhill and Alcock 1983). Female choice likely occurs to some degree in odonates because females can refuse copulation by not lifting her abdomen to the male hemipenis, can differentially use the sperm from different males and can choose to leave a male's territory before ovipositing (if contact mate-guarding is not involved) (Fincke 1997).

Most studies of selection in odonates have investigated the presence of directional, but not stabilising selection (Thompson and Fincke 2002). If overall directional selection were the norm, then species would continually be getting larger or smaller. Since the average size of species tends to stay relatively stable over long periods, we must assume that overall stabilising, rather than directional, selection is the norm in nature. Five odonate selection studies have found stabilising selection on body size with respect to measures of lifetime reproductive success (Banks and Thompson 1985b; Fincke 1982, 1988; Moore 1990; Stoks 2000), but the sample sizes necessary to detect stabilising selection are large, and these are the only selection studies of odonates to have found such results (Thompson and Fincke 2002). Further, most studies do not compare selective events between episodes, such as between generations or between natural and sexual selection. When sexual and natural selection are compared within a population, conflicting selection pressures are often found due to trade-offs between survival and reproduction, leading to fluctuating selection (i.e., Anholt 1991; Schluter et al. 1991). Stochastic variables such as weather, food supply and predator levels affect selection mechanisms by altering the underlying physical condition of the population and the allocation of energetic resources to traits important in reproductive success and survival (condition dependence - Rowe and Houle 1996). Consequently, selection on mating success may be weaker in times of environmental stress because fewer individuals survive to sexual maturity.

No single study has compared selection among territorial and non-territorial odonate species concurrently in the field, and few have compared selection between episodes (e.g., Anholt 1991). A recently published meta-analysis of fitness and body size in mature odonates found body size was correlated with mating rate, territorial success and lifetime mating success in territorial males, and with lifetime mating success in non-territorial males, but not with mating rate (Sokolovska et al. 2000). Further, the effect size of body size on lifetime mating success was greater in territorial than non-territorial males. These results agree well with expectations, but the data set was relatively small. The species were over-represented by the predominantly non-territorial damselfly family Coenagrionidae. Further, the analysis was biased towards studies of linear selection and did not consider the possibility of stabilising selection (Thompson and Fincke 2002).

This study expands the data set and includes species in which selection has not yet been measured. My objective was to compare sexual size dimorphism and sexual selection among territorial and non-territorial odonate species to test the predictions made by theory. To achieve this, I conducted an observational field experiment in the summers of 1998 and 1999 at Galiano Island, British Columbia where I measured the relationship between phenotype and mating success in males of two non-territorial (*Lestes congener* and *Lestes disjunctus*) and one territorial (*Sympetrum pallipes*) odonate.

Study species

Lestes congener and *L. disjunctus* damselfly males engage in scramble competition for females. Males and females typically encounter each other at the oviposition site, usually the pond from which they emerged at metamorphosis (Corbet 1999). Males appear to encounter females by chance, but increase the probability of encounter by maximizing time spent at the oviposition site. Because males engage in scramble competition, sexual selection on body size should be weak or non-existent.

Sympetrum pallipes is a territorial dragonfly species in which males compete to control access to suitable oviposition sites by females. Oviposition sites are a limiting resource and odonates choose preferential sites (Van Buskirk 1986; Waage 1987; Wildermuth 1998; Wolf and Waltz 1988) based mainly on visual cues (Corbet 1999). Females may judge the quality of the oviposition site before copulation, but in at least some species, copulation precedes the choice of oviposition site (Alcock 1990). It is therefore unclear whether females choose mates based on characteristics of the male (Andersson 1982; Moore 1988) or the characteristics of the resources he controls (i.e., Gwynne 1984; Thornhill 1976, 1980).

Not all males are able to gain control of territories; those that do (Alcock 1990) usually realize much greater mating success than others (Fincke 1992; Ito 1960; Plaistow and Siva-Jothy 1996; Tsubaki and Ono 1987). Intramale competition for territories is therefore intense. Establishing and defending territories against aggressive conspecifics is energetically costly (Marden and Waage 1990) and should favour larger individuals (with larger energy reserves) that are able to repel smaller individuals. I therefore predict selection for large body size in male *S. pallipes*.

Materials and Methods

Field observations

I captured and released sexually mature males at the same site described in Chapter 1. I weighed, measured and marked individuals consistent with the methods outlined therein. In order to increase sample sizes in 1999, I captured, weighed and measured some individuals but did not mark them. I preferentially captured mating males because they were less numerous than solitary males. Measuring and marking individuals was a larger limiting factor than the presence of solitary males, except for male *L. disjunctus* in 1999.

I recorded the date and mating status upon capture and recapture for each individual. Multiple matings were recorded for many individuals, but since I was not confident that I observed every mating occurrence, individuals were assigned a dichotomous fitness outcome: mated or unmated. This allowed greater confidence in the data because if an individual mated several times, I was likely to observe at least one of those matings.

Mating in odonates occurs at or near the oviposition site (Corbet 1980), for most but not all species. I therefore spent most of my observation time at, or close to, the pond. However, I also made regular observations away from the pond. Individuals were regularly captured away from the pond, but no mating pairs were observed more than about 30m from the pond.

I also made behavioural observations of marked male *S. pallipes* in order to determine if body size had an effect on the probability of holding a territory. If an individual was observed maintaining a territory against aggressive conspecifics, it was classified as territorial. I used no specific time measure in determining territoriality. If an individual was clearly subordinate or had unclear behaviour, it was classified as non-territorial. Those individuals whose territorial status could not be confidently classified, such as those that were only observed while mating, were not included in the data set.

Statistical methodology

Variable selection

Consistent with Chapter 1, I used the first principal component (PC1) of the correlation matrix of abdomen and wing length and mass as my measure of overall body size. Body size at emergence tends to decline over the season (Falck and Johansson 2000; Koenig and Albano 1987; Van Buskirk 1987). In this study, date of emergence had a significant effect on body size at emergence in all groups where $n>40$ (e.g., male *L. congener*, 1999: n=68, r^2=0.163, P=0.001; male *S. pallipes*, 1999: n=208, r^2=0.397, P<0.0001,). In mature individuals, date of capture was related to body size (e.g., male *L. congener*, 1999: n=140, r^2=0.031, P=0.037,) and the probability of being captured while mating in about one-half of the groups (e.g., male *S. pallipes*, 1999: n=171, r^2=0.025, P=0.0415). Where the results were significant, individuals tended to be smaller later in the season. Declining size over the season was taken to be the effect of declining size at emergence because size is fixed at emergence and mass did not decline with age (e.g., male *L. congener*, 1999: n=22, r^2=0.003, P= 0.815,), although the age of few individuals was known. Because of the effect of date on body size, it was included in all models.

Sexual Size Dimorphism

I also wanted to compare sexual size dimorphism (SSD) among species and years and body size between years within each species. Results from separate principal component analyses cannot be directly compared, however, because the loadings for each year are not identical. For each comparison I therefore performed a principal component analysis on the grouped data. For example, to compare SSD between *L. congener* and *L. disjunctus*, I ran a PC analysis with abdomen and wing length and mass as variables on data combined from both years and both species. I corrected for date by running a regression of PC1 against date and used the residuals in the analyses.

I tested for the difference in SSD between years and between species using ANOVA. Size was log transformed prior to analysis to account for dimorphism as a ratio. For between-years comparisons, I used the formula: size~year+sex+year:sex, and for between species comparisons, I used size~species+sex+species:sex. The significance of the interaction term indicates whether there was a difference in SSD between years or species.

I used two-tailed t-tests to test for the absolute differences in abdomen and wing lengths and mass, and the relative difference in overall body size, between years within sex and between sexes within species.

Selection on mating success

I estimated reproductive success by mating success. One record was created for each individual. I used mean mass for multiple recaptures because mass varied over time.

Selection surfaces were first estimated for body size and wing loading for each group using a cross-validated cubic spline program supplied by Dolph Schluter (GLMS, version 1, 1988). The cubic spline is a non-parametric approach to visualizing selection curves (Schluter 1988). The cubic spline provides a more accurate estimate of the fitness function than linear or quadratic regression because it is not restricted to symmetrical shapes, and can therefore indicate the presence of local modes or dips (Brodie et al. 1995; Schluter 1988). It describes the expected fitness of alternative phenotypes, as opposed to the selection coefficients of Lande and Arnold (1983), which measure the effects of the fitness function on the phenotype distribution (Schluter 1988). The program uses generalized cross-validation (GCV) to search for the value of the smoothing parameter (λ) that returns the lowest GCV score. It then performs a bootstrap sample using the most appropriate λ to estimate the shape of the curve, with 95% confidence intervals. Due to the effect of date on body size and wing loading, I first regressed each trait against date, then used the regression residuals as the fitness estimates.

Logistic regressions were also performed to estimate the strength and direction of sexual selection. Logistic regression is a more appropriate technique than multiple linear regression for these data because they are binomially distributed, and logistic regression constrains fitness predictions to fall between one and zero. Additionally, nonnormally distributed regression errors invalidate traditional inference techniques and can falsely suggest nonlinear selection surfaces (Janzen and Stern 1998). Following Janzen and Stern (1998), the regression coefficients were transformed to be comparable to multiple linear regression coefficients proposed by Lande and Arnold (1983), which are frequently used in selection experiments.

Model Selection

I tested for directional and variance selection on body size (PC1) in males of all three species. I considered wing loading (mass / wing length) as an alternative to Principal Components of body size measures, but it did not provide additional explanatory power. Consequently, I used body size only in selection analyses of mating success. The candidate models sets were otherwise identical to those used in Chapter 1. This created a set of six candidate models for each group (see Tables 2.3 and 2.4).

I also tested for a correlation between phenotype and territoriality in male *S. pallipes* by testing the same models with territorial status (observed holding a territory or not) as the fitness outcome. I then tested whether a territorial male was more likely to be observed mating than a non-territorial male using a Chi-square test. Since exoskeleton size is fixed at emergence, mass proportional to body size should be a good predictor of flight muscle tissue and fat reserves, which are important in extended territorial disputes (Marden 1988; Marden and Rollins 1994; Marden and Waage 1990). Further, the proportion of mass to wing length (hereafter called wing loading) should likely have an effect on an individual's maneuverability (Crompton et al. 2003). I therefore chose to use not only overall body size (PC1 scores) but also wing loading (mass/wing length) as my predictor variables for territorial probabilities in males of the territorial dragonfly, *S. pallipes*. This created a set of nine candidate models for this analysis (see Table 2.4).

The best models from each group were chosen based on the Akaike Information Criterion (AIC - Akaike 1973), which applies the principle of parsimony to choose the most appropriate model from a set of biologically relevant models (Burnham and Anderson 1998). The AIC uses the Kullback-Leibler discrepancy to measure the distance between the "true" model (i.e., if all parameters were known) and each candidate in a set of proposed models. The model with the lowest AIC value will be the best approximation of "truth". The AIC introduces parsimony by imposing a penalty based on the number of parameters estimated because too many will make a model unsuitable for inference.

Results

Principal components analysis

Abdomen length, wing length, and mass all had similar strong positive loadings on PC1 (Table 2.1). PC1 therefore provides a good measure of overall body size. PC1 accounted for between 48 (*L. disjunctus*, 1998) and 70% (*L. disjunctus*, 1999) of the total variance in body size measures. Table 2.1 also shows mean wing loading values with standard deviations.

Body size comparison between years

Lestes congener were larger overall in 1999 than in 1998 while *S. pallipes* were smaller; the difference in *L. disjunctus* was narrowly non-significant at P=0.052 (Table 1.6). This observation is supported by comparison of individual metric traits between the years. Male *L. congener* had 0.7mm longer abdomens (t = -11.211, df = 365, P < 0.0001) and 1.0mm longer wings (t = -9.789, df = 365, P < 0.0001) and were 7.6mg heavier at emergence (t = -9.019, df = 99, P < 0.0001) and 7.2mg heavier at maturity (t = -13.525, df = 365, P < 0.0001) in 1999 than 1998. *L.* disjunctus had 0.3mm longer wings in 1999 (t = -2.112, df = 317, P = 0.035), but other measures did not change. Male *S. pallipes* had 0.6mm shorter abdomens (t = 9.108, df = 487, P < 0.0001) and 0.1 mm shorter wings (t = 14.230, df = 487, P < 0.0001), and were 13.5mg lighter (t = 7.835, df = 487, P < 0.0001) in 1999 than 1998 (Table 2.1).

Wing loading values were more highly conserved between years than overall body size, but the patterns were similar (Table 1.6). Both male *L. congener* and *L. disjunctus* had larger wing loading values in 1999 than in 1998. In contrast, wing loading values were similar in *S. pallipes* between years, in spite of the highly significant difference in body size.

Sexual size dimorphism at emergence and sexual maturity

Females were larger than males at emergence and maturity in both *Lestes* species (Table 2.1). Female *Lestes* had shorter abdomens and longer wings in both years. Sexual size dimorphism (SSD) was greater at maturity because females gained more mass over the maturation period than males.

Table 2.1. Sexual size dimorphism at emergence and sexual maturity for all species, 1998 and 1999. Values shown are means ± standard deviations. Since skeletal size is fixed at emergence, teneral and mature data have been combined in groups in which teneral numbers are adequately large (*L.* congener, 1998 and 1999, *S.* pallipes, 1999). Metric traits used in t-test comparisons were corrected for date by taking the residuals of the trait regressed against date. *n*=teneral/mature.

	abdomen (mm)	*wing (mm)*	*mass (mg)*	
			emergence	*maturity*
1998				
Lestes congener				
Females (*n* = 45 / 186)	26.84 ± 1.07	21.04 ± 0.88	34.00 ± 4.16	63.37 ± 9.11
Males (*n* = 34 / 226)	28.51 ± 0.91	19.70 ± 0.97	30.44 ± 3.24	40.51 ± 3.83
F/M	**0.94**	**1.07**	**1.12**	**1.56**
	t = -18.60	*t* = 15.92	*t* = 4.81	*t* = 34.78
	df = 490	*df* = 488	*df* = 77	*df* = 414
	P < 0.0001	*P* < 0.0001	*P* = 0.0001	*P* < 0.0001
Lestes disjunctus				
Females (*n* = 9 / 127)	27.76 ± 0.86	21.87 ± 0.67	42.00 ± 9.03	71.09 ± 9.19
Males (*n* = 5 / 254)	29.34 ± 1.07	20.40 ± 0.95	36.25 ± 5.12	47.77 ± 4.17
F/M	**0.95**	**1.07**	**1.16**	**1.49**
	t = -14.57	*t* = 15.65	*t* = 1.17	*t* = 34.06
	df = 381	df = 382	*df* = 11	df = 379
	P < 0.0001	*P* < 0.0001	*P* = 0.2652	*P* < 0.0001
Sympetrum pallipes				
Females (*n* = 8 / 176)	24.32 ± 0.97	26.57 ± 1.05	71.25 ± 12.33	229.76 ± 28.77
Males (*n* = 6 / 311)	24.26 ± 0.96	26.92 ± 0.89	122.00 ± 49.82	185.77 ± 17.84
F/M	**1.00**	**0.99**	**0.58**	**1.24**
	t = 0.66	*t* = -3.81	*t* = -2.81	*t* = 21.03
	df = 486	df = 485	*df* = 12	df = 496
	P = 0.51	*P* = 0.0002	*P* = 0.0159	*P* < 0.0001
1999				
Lestes congener				
Females (*n* = 75 / 195)	28.13 ± 1.11	22.22 ± 0.77	42.35 ± 4.55	71.98 ± 8.39
Males (*n* = 68 / 144)	29.63 ± 1.22	20.73 ± 0.76	38.07 ± 4.34	47.67 ± 6.37
F/M	**0.95**	**1.07**	**1.11**	**1.51**
	t = -14.12	*t* = 21.32	*t* = 5.70	*t* = 29.18
	df = 481	*df* = 481	*df* = 139	df = 338
	P < 0.0001	*P* < 0.0001	*P* < 0.0001	*P* < 0.0001
Lestes disjunctus				
Females (*n* = 8 / 38)	27.89 ± 1.30	22.16 ± 1.01	52.62 ± 1.43	72.82 ± 10.66
Males (*n* = 6 / 67))	29.22 ± 1.17	20.68 ± 1.04	45.83 ± 4.71	48.69 ± 4.43
F/M	**0.95**	**1.07**	**1.15**	**1.50**
	t = -5.41	*t* = 7.11	*t* = 2.89	*t* = 16.26
	df = 103	df = 103	*df* = 12	df = 103
	P < 0.0001	*P* < 0.0001	*P* = 0.0135	*P* < 0.0001
Sympetrum pallipes				
Females (*n* = 217 / 136)	23.64 ± 1.10	25.38 ± 1.06	91.29 ± 14.48	207.28 ± 27.78
Males (*n* = 208 / 182)	23.62 ± 0.89	26.86 ± 1.03	103.68 ± 9.24	172.30 ± 17.64
F/M	**1.00**	**0.94**	**0.88**	**1.20**
	t = 0.27	*t* = -6.26	*t* = -8.93	*t* = 13.69
	df = 743	*df* = 743	*df* = 422	df = 316
	P = 0.786	*P* < 0.0001	*P* < 0.0001	*P* < 0.0001

Table 2.2. ANOVA results comparing sexual size dimorphism in mature individuals between years within species (size~year+sex+year:sex). Size is estimated by the first principal component of the correlation matrix of abdomen and wing length and mass on the combined data in each group, and was corrected for date by using the residuals of size regressed against date. Size was log transformed prior to analysis to account for dimorphism as a ratio.

	df	Sum of Sq	F Value	Pr(F)
Lestes congener				
sex	1	31.8129	1216.524	<0.0001
year	1	1.81898	69.558	<0.0001
sex:year	1	0.0002	0.008	0.929774
residuals	743	19.42994		
Lestes disjunctus				
sex	1	23.73465	1598.295	<0.0001
year	1	0.00393	0.265	0.607079
sex:year	1	0.00109	0.073	0.786439
residuals	478	7.09829		
Sympetrum pallipes				
sex	1	1.63306	21.8819	<0.0001
year	1	10.04776	134.6336	<0.0001
sex:year	1	0.21322	2.8571	0.091365
residuals	796	59.40579		

S. pallipes females had shorter wings than males, but abdomen length did not differ between the sexes (Table 2.1). Males were heavier and larger overall than females at emergence, but smaller at maturity, again due to larger mass gain by females over the maturation period. Two very heavy teneral males (179 and 185mg) skewed the sampling distribution in 1998; results of the 1999 teneral mass comparison are more likely repeatable, due to the much larger sample size.

SSD in metric traits was highly conserved between years, as shown by the similarity in female/male ratios between years within each species (Table 2.1). Not surprisingly, when male and female measures were combined in a principal components analysis for each species and PC1 was compared between sexes, overall size was significantly different in all species (these results are not presented here). Although size was greater in 1999 for *L. congener* and *S. pallipes*, there was no difference in SSD between years (sex:year – Table 2.2).

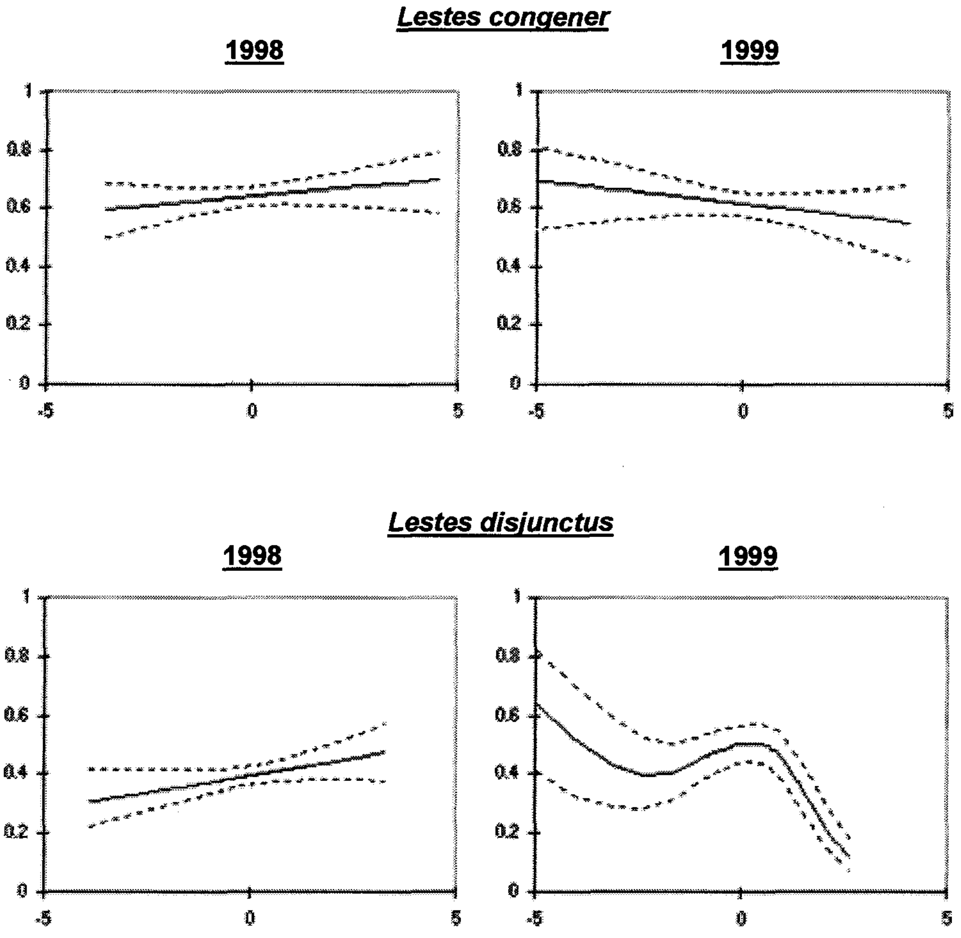
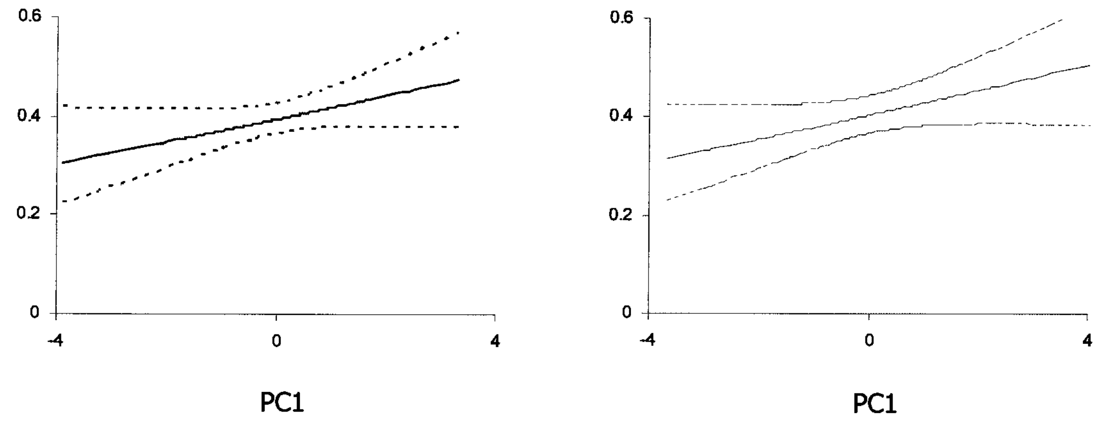


Figure 2.1. Cubic spline selection curves estimating expected mating success as predicted by body size for male *Lestes congener* and *Lestes disjunctus* in 1998 and 1999. x-axes represent relative body size (residuals of PC1 regressed against date); y-axes represent expected probability of mating; solid curves are the best estimates of the selection curve, dashed lines are 95% bootstrapped confidence intervals (r=10,000). GLMS program provided by Dolph Schluter (Schluter, 1988).

Mating success in males

There was little support for directional or stabilizing selection in *L. congener* or *L. disjunctus* in either year. Cubic spline selection curves suggest no selection on body size in *L. congener* in 1998 or 1999; the slopes are very near zero with narrow confidence boundaries (Figure 2.1). This conclusion is supported by logistic regression results: the null model has the greatest support in both years (Table 2.3). There was no evidence for selection in male *L. disjunctus* in 1998, but in 1999, large *L. disjunctus* in 1999 appeared less likely to achieve mating success than



Sympetrum pallipes mating success

1998

1999

Sympetrum pallipes territorial success, 1999

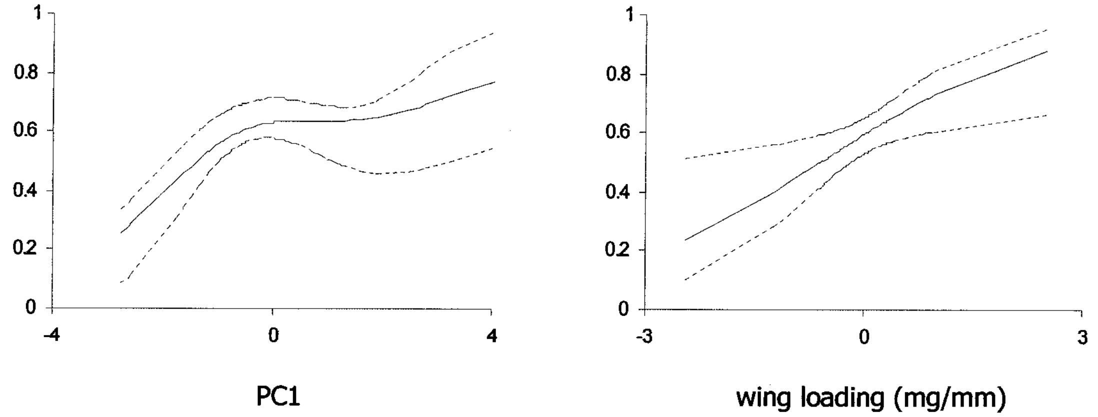


Figure 2.2. Cubic spline selection curves estimating expected mating success as predicted by body size (PC1) and estimated territorial success as predicted by body size and wing loading for male *Sympetrum pallipes*. Residuals of the regressions of PC1 and wing loading values against date are used here to account for the effect of date on these traits. y-axes represent the expected probability of mating or territorial success; solid lines are the best estimate of the selection curve, dashed lines are 95% bootstrapped confidence intervals (r=10,000). GLMS program provided by Dolph Schluter (Schluter, 1988).

average or small individuals (Figure 2.1). Logistic regression results suggest an effect of date and body size on mating probabilities in *L. disjunctus* in both years – the date model has the most support in both years and the null model has the least (Table 2.3). Transformed selection gradients, however, show that mating success was almost exclusively an effect of date – individuals had a higher probability of mating success later in the year in 1998 and earlier in 1999

(Table 2.5). Overall, there was little evidence for selection on body size in this species. Models incorporating PC1 were the second best models in both years but the confidence intervals overlapped zero by a wide margin. Notably, however, the sign on the PC1 selection gradients again changes between years. Unexpectedly, it is positive in 1998 when the mean body size of the population was larger and the sign was negative in 1999 when the mean size was smaller.

Table 2.3. Mating selection logistic regression AIC results for *Lestes congener* and *L. disjunctus*, 1998 and 1999, including -2log likelihood values and number of parameters (*K*). AICc values represent the fit of the model to the data, corrected for small sample sizes; lower values suggest a better fit. ΔAICc values show the distance in AICc values from the lowest score. AICc weights represent the relative power of each model to describe the data, given the current set of models.

Rank		*-2log(L)*	*K*	*AICc*	*ΔAICc*	*AICc weights*
	Lestes congener, 1998					
1	Null	294.038	1	296.06	0	0.54
2	Date	293.992	2	298.05	1.99	0.20
3	PC1+Date+PC1:Date	290.986	4	299.17	3.11	0.11
4	PC1+Date	293.702	3	299.81	3.75	0.08
5	PC1+PC1^2+Date+PC1:Date	290.949	5	301.22	5.17	0.04
6	PC1+PC1^2+Date	293.693	4	301.88	5.82	0.03
	Lestes congener, 1999					
1	Null	189.580	1	191.61	0	0.47
2	Date	188.758	2	192.84	1.24	0.26
3	PC1+Date	188.471	3	194.64	3.04	0.10
4	PC1+Date+PC1:Date	186.897	4	195.19	3.58	0.08
5	PC1+PC1^2+Date+PC1:Date	185.801	5	196.24	4.63	0.05
6	PC1+PC1^2+Date	188.328	4	196.62	5.01	0.04
	Lestes disjunctus, 1998					
1	Date	322.489	2	326.54	0	0.51
2	PC1+Date	321.724	3	327.82	1.28	0.27
3	PC1+Date+PC1:Date	321.691	4	329.86	3.32	0.10
4	PC1+PC1^2+Date	321.717	4	329.88	3.34	0.10
5	PC1+PC1^2+Date+PC1:Date	321.680	5	331.93	5.39	0.03
6	Null	335.678	1	337.69	11.16	0
	Lestes disjunctus, 1999					
1	Date	81.368	2	85.56	0	0.47
2	PC1+Date	80.120	3	86.50	0.95	0.29
3	PC1+PC1^2+Date	79.967	4	88.61	3.06	0.10
4	PC1+Date+PC1:Date	80.107	4	88.75	3.20	0.10
5	PC1+PC1^2+Date+PC1:Date	79.965	5	90.95	5.39	0.03
6	Null	91.669	1	93.73	8.18	0.01

Table 2.4. Mating selection logistic regression AIC results for male *Sympetrum pallipes*, 1998 and 1999, including -2log likelihood values and number of parameters (K). AICc values represent the fit of the model to the data, corrected small sample sizes; lower values suggest a better fit. ΔAICc values show the distance in AICc values from the lowest score. AIC weights represent the relative power of each model to describe the data, given the current set of models. wl=wing loading.

Rank		*-2log(L)*	*K*	*AICc*	*ΔAICc*	*AICc weights*
	***Sympetrum pallipes* mating success, 1998**					
1	PC1+Date	354.280	3	360.36	0	0.34
2	Date	357.013	2	361.05	0.69	0.24
3	PC1+Date+PC1:Date	353.574	4	361.71	1.35	0.18
4	PC1+PC1^2+Date	353.754	4	361.89	1.53	0.16
5	PC1+PC1^2+Date+PC1:Date	353.159	5	363.36	3.00	0.08
6	Null	394.712	1	396.73	36.36	0
	***Sympetrum pallipes* mating success, 1999**					
1	PC1+PC1^2+Date+PC1:Date	214.241	5	224.61	0	0.46
2	PC1+Date+PC1:Date	216.556	4	224.80	0.19	0.42
3	Date	225.278	2	229.35	4.74	0.04
4	PC1+PC1^2+Date	221.249	4	229.49	4.88	0.04
5	PC1+Date	224.476	3	230.62	6.01	0.02
6	Null	229.610	1	231.63	7.03	0.01
	***Sympetrum pallipes* territorial success, 1999**					
1	wl+Date	87.808	3	94.16	0	0.27
2	Date	90.899	2	95.07	0.92	0.17
3	PC1+Date	89.211	3	95.56	1.40	0.14
4	PC1+PC1^2+Date	87.585	4	96.17	2.02	0.10
5	wl+wl^2+Date	87.597	4	96.19	2.03	0.10
6	wl+Date+wl:Date	87.795	4	96.38	2.23	0.09
7	PC1+Date+PC1:Date	99.946	4	97.53	3.38	0.05
8	PC1+PC1^2+Date+PC1:Date	87.525	5	98.42	4.27	0.03
9	wl+wl^2+Date+wl:Date	87.560	5	98.46	4.30	0.03
10	Null	98.872	1	100.93	6.77	0.01

I found conflicting evidence for selection on body size relative to mating success in male *S. pallipes*. Cubic spline selection curves show possible weak positive directional selection on body size in both years (Figure 2.2). This is supported by logistic regression results in 1998: the selection gradient for PC1 is positive but weak, suggesting that large body size gives male *S. pallipes* a slight advantage in the probability of mating success (Table 2.4). While selection curves are similar for 1998 and 1999, logistic regression results show large differences. The two best models in 1999 both include PC1, Date and a PC1:Date interaction term and together account for an AICc weight of 0.88 (Table 2.4). Further, they have AICc values over 4 units lower than the next best model and thus have very strong support. Transformed PC1 selection gradients, however, are large and negative in both models (Table 2.5), in direct contrast with selection curves. Males were more likely to mate later in the season in both years; large positive interaction terms show that small males have an advantage early in the season but large males have an advantage late in the season.

***Probability of holding a territory in male* Sympetrum pallipes**

Forty-three of 73 marked individuals were observed maintaining territories and defending them against aggressive conspecifics. Of these, 14% (n = 6) were observed to change their status between clearly territorial behaviour and not. The maximum duration of territorial behaviour displayed by any individual was 24 days, but ownership was likely not continuous over this period. Territorial individuals were more likely to be observed mating than non-territorial individuals (χ^2=10.076, df =1, *P*=0.0015).

The effect of size on the probability of establishing and maintaining a territory in *S. pallipes* in 1999 is convincing; selection curves show a diminished probability of territorial success for small individuals and strong positive directional selection for individuals with large wing loading values (Figure 2.2). Logistic regression results give greatest support to positive directional selection on wing loading as well as some support to models including date and PC1; the null model has the least support of any (Table 2.4). Transformed selection gradients are positive but relatively weak on wing loading and the confidence interval narrowly overlaps zero (Table 2.5). Date again also had an effect, with fewer individuals realizing territorial success later in the season (Table 2.5). There was some evidence of stabilizing selection on body size shown in the selection curves (Figure 2.2), but regression results did not support this conclusion, perhaps due to relatively low sample size (*n*=73) of individuals that could be classified as clearly territorial or non-territorial.

Table 2.5. Transformed logistic regression mating success selection gradients. Gradients are beta parameters provided by program MARK that estimate the effect of body size on survival and were transformed according to Janzen and Stern (1998) and are directly comparable to selection gradients as proposed by Lande and Arnold (1983).

	estimate	*SE*	*LCL*	*UCL*
Lestes disjunctus				
1998				
mating success~Date				
Date	0.270	0.076	0.120	0.419
mating success~PC1+Date				
PC1	0.067	0.076	-0.083	0.216
Date	0.279	0.077	0.128	0.431
1999				
mating success~Date				
Date	-0.431	0.147	-0.719	-0.142
mating success~PC1+Date				
PC1	-0.149	0.135	-0.413	0.115
Date	-0.455	0.151	-0.750	-0.160
Sympetrum pallipes				
1998				
mating success~PC1+Date				
PC1	0.119	0.072	-0.023	0.261
Date	0.450	0.077	0.299	0.601
1999				
mating success~ PC1+PC1^2+Date+PC1:Date				
PC1	-0.509	0.240	-0.979	-0.039
PC1^2	-0.117	0.040	-0.195	-0.039
Date	0.155	0.072	0.014	0.295
PC1:Date	1.201	0.602	0.022	2.380
mating success~ PC1+Date+PC1:Date				
PC1	-0.661	0.292	-1.238	-0.094
Date	0.193	0.092	0.012	0.373
PC1:Date	0.785	0.295	0.207	1.363
***Sympetrum pallipes* territorial success**				
1999				
territorial success~wing loading+Date				
wing loading	0.192	0.118	-0.039	0.423
Date	0.317	0.122	0.078	0.557

Discussion

Consistent with predictions, there was little or no sexual selection on male *L. congener* or *L. disjunctus*. Also consistent with predictions, large size and wing loading values in male *S. pallipes* conferred a territorial advantage and territorial males had a greater mating success. Large size increased mating probabilities in *S. pallipes* in 1998 but there was correlational selection in 1999 in which small males had a mating advantage early in the season but large males had an advantage late in the season. Changes in overall body size and the direction of selection between years in two of three species underscore the importance of measuring selection on more than one episode to help understand long-term averages.

Sexual size dimorphism

As predicted, sexual size dimorphism (SSD) was greater in *L. congener* and *L. disjunctus* than it was in *S. pallipes*. Female *Lestes* were larger than males at emergence and gained more relative mass with the result that SSD was greater at maturity than at emergence in both years. Female *S. pallipes* were lighter than males at emergence but heavier at maturity in both years. At sexual maturity, *Lestes* females were 50% heavier than males while *S. pallipes* females were only 20% heavier (Table 2.1).

These results are consistent with SSD in other odonate species. In a thorough survey, Anholt et al. (1991) found that non-territorial zygopteran (damselfly) female/ male mass ratios ranged from 0.86 to 1.29 (median=1.02, 1.08, *n*=4 species) at emergence to 0.99 to 1.97 (median=1.50, 1.52, *n*=14 species) at maturity, while in anisopterans (dragonflies) mass ratios ranged from 0.86 to 1.21 (median=0.97, *n*=13 species) at emergence and 0.90 to 1.67 (median=1.22, 1.23, *n*=42 species) at maturity. While these data are not phylogenetically controlled, territoriality is more prevalent in Anisoptera than Zygoptera; this therefore indicates an effect of mating system on SSD. SSD in *L. congener* and *L. disjunctus* is very similar to other zygopterans at maturity (1.49 to 1.56), and SSD in *S. pallipes* was at the median for size at maturity (1.20 to 1.24). These data are consistent with the hypothesis that males of territorial species gain proportionately more mass over the maturation period than males of non-territorial species, with the result that SSD is larger in non-territorial species at maturity.

These results also agree well with the Ghiselin-Reiss small male hypothesis (Ghiselin 1974). Further empirical support for this hypothesis has been found in both water striders (Blanckenhorn et al. 1995) and other damselflies: male mating success in *Ischnura elegans* was negatively correlated with body size, as estimated by wing length (Carchini et al. 2000); and small *Enallagma boreale* males had higher mating success than large males, but a lower survival rate from emergence to sexual maturity (Anholt 1991). These results are also consistent with Rensch's rule (Rensch 1960), which stipulates that in taxa in which females are the bigger sex, SSD decreases with body size (hypoallometry). One argument used to explain this phenomenon is the presence of stronger selection for large body size in males than females (Clutton-Brock et al. 1977; Fairbairn and Preziosi 1994; Leutenegger 1978; Maynard Smith 1977; Webster 1992). However, models suggest this is only possible if SSD is not at equilibrium (Webster 1992). SDD in this study is remarkably similar between years, in spite of large changes in overall body size, suggesting SSD is at or near equilibrium. Thus, other hypotheses are necessary to explain the conformance with Rensch's rule among the species of this study. Since offspring size is affected by both male and female parental genotypes, large fathers tend to produce large daughters as well as large sons (Webster 1992); further, the effect of selection for large body size in males could be balanced by weak, non-existent or negative selection in females.

Small size is likely to be beneficial in *L. congener* and *L. disjunctus* because large size does not confer any mating advantage and mass gain is costly because it necessitates increased foraging activity which puts the animal at increased risk of predation. Predator avoidance through behaviour modification is common among animals (e.g., Kohler and McPeek 1989; Lima and Dill 1990; McPeek 1995; Sih 1982; Skelly and Werner 1990). Larval odonates reduce activity in the presence of predators (Koperski 1997; Schaffner and Anholt 1998) and faster-growing species suffer higher predation (McPeek et al. 2001). Among adult odonates, survival in immature adult *Enallagma boreale* was inversely correlated with mass gain (Anholt 1991), but no other studies have investigated this phenomenon in odonates.

Alternatively, in territorial species, large size is important in establishing and maintaining territories. High fat content is often correlated with mating success in males of territorial damselflies in the zygopteran genus *Calopteryx* (e.g., *Calopteryx maculata,* Maarden and Waage, 1990; Maarden and Rollins, 1994; *C. splendens xanthostoma,* Plaistow and Siva-Jothy, 1996). In male *C. maculata,* for example, winners were fatter in 68% of short contests and 95% of long contests, and the duration of disputes was positively correlated with average fat content of the contestants (Marden and Waage 1990).

Territoriality is energetically costly. Territorial males of *Pachydiplax longipennis* spent about 85% of their total available energy in defense of their territories (Fried and May 1983), and escalated disputes that displace residents cost both participants 40-50% of their energy reserves (Corbet 1999). Defending territories also requires frequent patrol flights in many species. This causes additional energy requirements in large males because the energetic costs of slow and hovering flight increases with size (Weis-Fogh 1977). Further, males of some species rarely forage while defending territories (Fried and May 1983; Marden and Waage 1990) and thus have no opportunity to renew energy stores while actively territorial.

Since mass gain is risky, and males of territorial species gain more mass over the period of maturation than males of non-territorial species, mass must be of crucial importance to males of territorial species because survival probabilities are compromised to improve chances at mating success.

Differences between years

Marked differences were seen in overall body size between 1998 and 1999 in all species. Male *L. congener* were larger in 1999; male *L. disjunctus* were also larger but the difference was narrowly non-significant. In contrast, male *S. pallipes* were smaller in 1999. Females of all species showed similar patterns: female *L. congener* were 0.87*SD larger in 1999, while female *L. disjunctus* were 0.42*SD larger and female *S. pallipes* were 0.75*SD smaller. This was very consistent with changes seen in males: male *S. pallipes* were about 0.75*SD smaller in 1999 while male *L. congener* were about 0.9*SD larger.

Body size changes between years of this magnitude are not rare (e.g., Anholt 1991; Michiels and Dhondt 1989), yet the conservation of SSD in spite of large annual changes in body size is a surprising result. Two explanations are plausible. First, selection on one sex may be correlated with selection on the other. This is known to occur where the body size of one sex imposes limitations on the body size in the other. For example, if males have to carry females during courtship or mating or have to physically coerce mating partners (Arnqvist 1992; Fairbairn 1990; Marden 1989b; Rowe 1992). In odonates, most species remain in tandem for much of the duration of copulation and oviposition; thus the size of successful male suitors may be constrained by the size of their mates. Further, coercion is important in at least some species (Fincke 1997; Forbes 1991; Ruppell 1989). During this study, I witnessed female *S. pallipes* that appeared to be actively resisting courtship by males; this has been observed in other species (e.g., Ruppell 1989). Second, phenotype is an expression of both genotype and environmental conditions. Since males and females are subject to the same environmental conditions and SSD was highly conserved between years, it is possible that while phenotype changed dramatically between years, genotype changed very little. This would suggest that either selection on body size in 1998 was either very weak or the sum of all selective pressures, including sexual selection and natural selection during the larval and adult stage, was stabilizing on body size.

Selection is rarely compared between episodes, but since environmental conditions such as weather can affect selection (Banks and Thompson 1985b; Harvey and Walsh 1993; Tsubaki and Ono 1987), and weather changes between years, it would not be surprising to find that the nature of selection would change between years. In the only previous study to examine selection in odonates in two successive years, earlier emerging *Enallagma boreale* females were more successful in one year and late emerging males and females were more successful the next year (Anholt 1991). These results have important implications for studies of selection that focus on only one episode, and help to explain the maintenance of size over time in spite of frequently strong directional selection pressures.

Probability of mating in Lestes *and* Sympetrum *males*

Although SSD was highly conserved and a large change in mean body size occurred between years, there was little evidence to suggest that body size had an effect on mating probabilities, except in *S. pallipes* in 1999.

Sexual selection theory suggests that males of non-territorial species should realize little benefit from large size. In contrast to expectations, several studies have found large size to be advantageous in males of non-territorial species. Two separate studies of *Ischnura graellsi*, each of which studied two populations, found higher success for larger males in one, but not both populations; however, the results in one of the studies were not significant when date of marking was used as a covariate (Cordero 1995; Rivera et al. 2002). Harvey & Walsh (1993) found that large males of this species had a higher mating success but they did not take the effect of the date of emergence on body size into account. While not classified as a territorial species, conspecific male *Coenagrion puella* display aggressive behaviour that results in either or both individuals leaving the rendezvous site (Moore 1995), and large size in this species may be more beneficial than those in which no aggressive behaviour occurs. In *Sympetrum danae*, a non-territorial dragonfly, large, active males had a higher mating success in both field enclosures and in the wild (Michiels and Dhondt 1991), but the authors cite aggressive male behaviour that, although perhaps not strictly territorial, suggests that direct male-male competition is occurring that is similar to conflicts seen in territorial males. Consequently, it is not surprising to find sexual selection for large size in these two species.

A recent meta-analysis of 33 studies of selection on body size in male odonates found that there was a significant, but small, benefit to large size in non-territorial males (Sokolovska et al. 2000), but the meta-analysis did not test for stabilizing selection and some of the studies included may have been inappropriate (see Thompson and Fincke 2002), leaving the results in doubt.

Since body size is typically conserved over time, stabilizing selection should be the norm, but too often this is not tested for (Thompson and Fincke 2002). Stabilizing selection on body size, through lifetime mating success, has so far been found in only three species of odonates, all of which were non-territorial (Banks and Thompson 1985b; Fincke 1982, 1988; Stoks 2000). For example, large male *Coenagrion puella* had greater longevity, but a lower daily mating rate than small males; however, the overall effect of size was that males at both ends of the size distribution were less likely to realize mating success (Banks and Thompson 1985b). Further, the effect on total lifetime mating success was very small (~2% of the daily variance in mating success) and weather was shown to have a major effect (Banks and Thompson 1985b).

There is some evidence to suggest that body size is maintained over the long term by fluctuating selection, in which the direction of selection changes between years or generations, depending on variables such as weather, predation and food levels. In this case, the phenotypic expression of genotype is affected by environmental variables, although the genotypic distribution itself remains relatively consistent. Thus, body size varies relative to condition (Rowe and Houle 1996). This may be the case, for example, in *L. disjunctus*. There was good evidence to show that males were larger in 1999 than 1998 (although narrowly non-significant at $P=0.052$). Concurrently, while confidence limits were wide, the sign on the sexual selection coefficient changed from positive in 1998 to negative in 1999, when individuals were relatively larger. This may be evidence that selection is responding to the change in the phenotypic distribution caused by environmental stochasticity. Further, conflicting selection pressures can occur within the lifespan of an individual. For example, large size may increase the probability of mating success, but decrease longevity (Schluter et al. 1991).

Body size had a small positive effect on mating probabilities in male *S. pallipes* in 1998. In 1999, small males had a mating advantage early in the season, but large males had an advantage late in the season. Several studies have tested for a correlation between body size and reproductive success in territorial male odonates (Koenig and Albano 1985; Marden 1989a; Moore 1990;

Tsubaki and Ono 1987; Van Buskirk 1987). In territorial male *Sympetrum rubicundulum*, the total number of days a male was present at the pond, but not wing length or date of emergence, was positively correlated with mating success, measured as the total number of matings observed, but mass was not included as a predictor variable (Van Buskirk 1987). Large size, but not wing length, had a positive effect on the success of territorial male *Libellula luctosa* in gaining access to a territory (Moore 1990); however, consistent with this study, Moore also found that although size improved a male's territorial competitiveness, it had no measurable effect on total sexual selection, estimated as the total number of ovipositions achieved by the male's mates. Similarly, in territorial *Plathemis lydia*, males with high flight muscle ratios (ratio of flight muscle mass to body mass) had disproportionately high short-term mating success, a relationship that was shown to be even more highly significant when males with weight belts were included in the analysis (Marden 1989a). Koenig and Albano (1985) found a weak but positive correlation between body length and mating success and a negative correlation between wing wear (a surrogate for age) and mating success in *Plathemis lydia*. However, in a later study of the same species, they also found that body size and wing length had no effect on the matings per hour on the pond, seconds of oviposition per mating or total seconds of oviposition, but the sample size was low (n = 21 to 48) (Koenig and Albano 1987). They suggest that there may be a trade-off between natural and sexual selection: more active males had a higher mating efficiency, but were at the pond for shorter periods of time, possibly due to the large amounts of energy burned while on the wing; alternatively, males with shorter hind wing lengths survived longer but had lower mating efficiency (Koenig and Albano 1987).

The change in the direction of selection on body size from negative to positive during the season in 1999 may have resulted from a change in density. Population sizes were not estimable using mark-recapture techniques due to large recapture heterogeneity, but I observed that as the angle of the sun became lower in the sky through the season, fewer sites were suitable for mating and oviposition. As a result, the density of males appeared to increase at the remaining suitable sites. Concurrently, the day length and temperature decreased with the season, thus decreasing the period of time over which mating was possible each day. This may have increased selection pressures on males because they had relatively more competitors and less time available than earlier in the season. The cost of death late in the season also decreases because it results in fewer missed mating opportunities. As a result, it appears that male-male competition increased late in the season in *S.* pallipes. Increased density of mature males at oviposition sites has been found to increase site attachment (Parr 1983; Poethke 1988), decrease the size of territories (Alcock 1989; Parr and Parr 1974; Waage 1972), or cause males to spend less time at their territories (Alcock 1989; Moore 1987) or adopt non-territorial strategies (Convey

1989; Forsyth and Montgomerie 1987; Moore 1987; Pajunen 1966; Tsubaki and Ono 1986; Waage 1972). Increased density can also lead to more territories being shared by two territorial males (Moore 1989) or increase the probability that inexperienced males will be expelled from a territory (Campanella and Wolf 1974), but an increase in the intensity of selection has not been found in other studies.

While males may be capable of coercing females or enticing them with high quality oviposition sites, once a tandem is formed, cooperation of the female is required to initiate copulation because she needs to raise her abdomen to meet the male's secondary genitalia. Thus, sexual selection in males may not arise exclusively from male-male competition, but may also occur through female choice. Females of various species have cues that indicate willingness or resistance to mating such as conspicuous flight (Kaiser 1985), wing signals (Fincke 1987; Waage 1984a), dislodging a male with forelegs (Koenig 1991; Ruppell 1989), resisting flight (Bick and Bick 1963), holding perches (Fincke 1986), shaking (Forbes and Teather 1994), or simply leaving a site without mating (Fincke 1992; Robertson 1982; Waage 1973). Strong evidence for female choice for large size (correlated with size of territory) has been found in *Megaloprepus coerulatus* (Fincke 1992) and for the width of wing pigments in *Libelulla luctosa* (Moore 1990). While it is not possible to determine the extent of female choice in phenotypic sexual selection in *S. pallipes* and its importance relative to male-male competition, evidence suggests that it does play a role in determining which males get to mate.

Body size and territorial success

Large wing loading values increased the probability of holding a territory in male *S. pallipes*. Wing loading can be seen as variation in mass relative to skeletal size. Much of the variation in mass in odonates consists of body fat and flight muscle tissue (Marden and Waage 1990). In territorial conflicts in *Calopteryx maculata*, winners had more body fat than losers 88% of the time, but body size or flight ability did not affect the outcome (Marden and Waage 1990). Further study showed that males likely assess each other's fat levels to decide the outcome of conflicts before physical energy limitations are reached (Marden and Rollins 1994). High proportions of flight muscle tissue increase flight performance (Marden 2000). Larger dragonflies also may be able to stay on the wing longer; in a study of various flying taxa, Harrison and Roberts (2000) found that, within species, mass-specific flight metabolism decreased with body size, but power output was constant or increased, with the result that efficiency increased with body size.

Body size also likely played a role with small individuals realizing poorer territorial success. Large size has been shown to be beneficial to territorial success in several studies (e.g., Fincke 1992; Michiels and Dhondt 1991; Miller 1983; Moore 1990). This is thought to be principally because territorial males engage in escalated intrasexual conflicts, the outcome of which determines an individual's right to hold territories and thus have access to females that attempt to oviposit there. Within a territorial species, territorial males are often larger than satellite males (Fincke 1984, 1992; Marden and Waage 1990; Moore 1990; Plaistow and Siva-Jothy 1996). While alternative mating tactics often occur, those males that establish and maintain territories usually realize much greater mating success than those that adopt alternative strategies, such as satellite or sneaker males (Fincke 1992; Ito 1960; Plaistow and Siva-Jothy 1996; Sokolovska et al. 2000; Thompson and Fincke 2002; Tsubaki and Ono 1987).

Territorial activity was not consistent throughout the season. As noted, male density appeared to increase late in the season. On several occasions, up to five males were observed perched on the same rock within less than 20cm of each other with no evidence of territorial activity. As a result, males may not have been able to control territories regardless of body size. About 15% of male *S. pallipes* were observed clearly exhibiting territorial activity in the first half of the season while only about 7% were observed doing so in the second half. In some cases, increased density may result in males attempting forced copulations, as has been observed in *Calopteryx haemorroidalis* (Cordero 1999). Apparent attempts at forced copulations were observed late in the season in 1999. Thus, there may have been a change in strategy in which males advertise their reproductive quality early in the season by the quality of their territory, and attempt to coerce matings late in the season. Body size may be a more important constraint during female coercion than in territoriality. If female choice is a large component of sexual selection in this species, then females would be choosing males based on the quality of their territory early in the season, but based directly on male characteristics late in the season. Alternatively, competition may be stronger later in the season because death has a lower cost in terms of missed mating opportunities.

Although territorial males were more likely to be observed mating than non-territorial males, large size was not shown to directly increase mating success. In fact, there was apparent selection for small size in 1999. Male *S. pallipes* were smaller in 1999 than in 1998. If selection in this species acts to maintain long-term body size equilibrium, as we would expect, then we should see selection for large size in 1999. Since there was evidence of selection for small size, this suggests that selection is relative to the available phenotype distribution, and that there is no long-term body size optimum maintained exclusively by sexual selection in this species.

Effects of weather

Dragonflies are only on the wing during good weather, and rain and cool temperatures can therefore decrease the opportunity for mating (e.g., Banks and Thompson 1985b; Harvey and Walsh 1993; Tsubaki and Ono 1987). For example, large territorial *Nannophya pygmaea* males held high-quality territories (those that attracted more females than others) for more days than smaller males, resulting in a higher lifetime mating success, but multiple regression analysis showed that variables related to weather condition explained most of the variance in mating success, not body size (Tsubaki and Ono 1987).

In 1999, the total precipitation over the flight season was nearly double that in 1998 (143mm v. 75.9mm), there were over 50% more days with rain (36 v. 22 days) and the average temperature over the period of the study was nearly 2°C lower (16°C v. 17.8°C) (weather data from Galiano North weather station, provided by Environment Canada). *Lestes* males were much larger in 1999 while *S. pallipes* males were much smaller. Weather could affect growth at various life stages including larval, immature adult and mature adult. It was not possible to test the correlation between weather and mating success because I did not know the life span of each individual and did not likely observe every mating occurrence for each individual.

In spite of large body size differences between the years, SSD was conserved and selection was weak or non-existent. This suggests that stochastic variables such as predators, food levels, weather or survival at various life stages were more important in determining immature and mature adult sizes than sexual selection.

Notes on methodology

Many mating occurrences were probably not observed, so that some proportion of the individuals classified as non-mating were erroneously classified. This would obscure the relationship between mated and non-mated individuals. Further, measures of short-term mating success can give incorrect conclusions due to tradeoffs between selection episodes (Banks and Thompson 1985b; Cordero 1995; Fincke 1986; Lande and Arnold 1983). Mating success can be a good predictor of reproductive success when most or all of the mating occurrences are observed (e.g., Vermette and Fairbairn 2002).

Given the likely occurrence of effective sperm competition in both *Lestes* and *Sympetrum*, however, mating success should equate to reproductive success, assuming females oviposit directly after copulation. Yet mating success may not be proportional to the number of surviving offspring a parent produces (Fincke and Hadrys, 2001). For example, fewer than half the mating adult *Megaloprepus coerulatus* produced any surviving offspring because larval survival was variable and depended upon "windows of opportunity" that provided the greatest probability of larval survival (Fincke and Hadrys, 2001). Further, there may be an optimum mating rate beyond which fitness decreases due to the effect of multiple matings on survival (Arnqvist and Nillson, 2000). If this is the case with odonates, then mating success as a binomial variable would be inadequate to estimate reproductive success. Data that include the total number of matings among males and the fecundity of their mates would likely increase the precision of future studies but would require large investments in effort.

Conclusion

This study has two major conclusions. First, body size is more important to males of territorial than non-territorial species. Further, while overall body size is important in males of territorial species, flight muscle ratios and energy reserves also likely play a critical role in determining territorial, and thus mating, success. Second, annual or generational changes in body size can be dramatic in spite of relatively weak selective pressures. This suggests that forces other than sexual selection such as weather or predator or prey levels, or natural selection during the larval or adult stage, can play a critical role in determining body size. Therefore, examination of selection over one episode only can give an incomplete or misleading picture of the overall direction of selection. This underscores the value of measuring selection over more than one episode or generation whenever possible.

General Discussion

I found that patterns of natural and sexual selection broadly agreed with predictions. However, large differences in body size between years were unexpected. Selection over the adult life stage was unable to explain the difference in body size from one year to the next. Therefore, changes in body size between years were either a result of strong selection during the larval stage or a result of unpredictable environmental variation.

In **Chapter 1**, I explored the interplay between mass gain and survival and the effect of mating system. As predicted, females gained more mass over the maturation period than males, with the result that sexual size dimorphism was greater at maturity than at emergence. Sexual differences in mass gain over the maturation period were lower in the territorial dragonfly, *S. pallipes*, with the result that sexual size dimorphism was smaller in this species. I predicted that as a result of this differential mass gain over the maturation period, females should have lower survival than males, but the difference should be smaller in *S. pallipes*. I found that female *L. congener* and *S. pallipes* had the lowest teneral survival while male *S. pallipes* had the next lowest survival, and male *L. congener* had teneral survival that was not detectably different from mature survival. These results thus agree well with predictions.

Groups with lower survival should also have a greater opportunity for selection (Crow 1958). Due to low sample sizes, I was only able to detect survival selection over the maturation period in female and male *L. congener* in both years and in female and male *S. pallipes* in 1999. Contrary to predictions, relatively weak negative directional selection was found in female *L. congener* in 1998 and none was found in 1999; further, selection gradients were weaker than in male *L. congener* in which there was strong negative selection on body size over the maturation period in 1998, but none detected in 1999. Selection on body size should have been strongest in female *S. pallipes*; however, I was not able to detect natural selection in this group, partly due to a low proportion of recaptured tenerals. The strongest evidence for selection over the maturation period was in male *S. pallipes* in 1999, which suggested strong positive linear selection on wing loading with equally strong stabilizing selection.

After maturity, daily survival rates varied from about 0.94 (male *S. pallipes*, 1998; female *L. disjunctus*, 1998) to about 0.98 (female *S. pallipes*, 1998 and 1999). No detectable differences were found between sexes in any species in either year, but there was substantial uncertainty in female recapture rates with the result that survival estimates were poor. I found negative directional selection on wing loading in female *L. congener* in 1998 and positive directional selection on wing loading in both years in male *L. congener*. Logistic regression results provided strong support for natural selection in female *S. pallipes*, but selection gradients were not interpretable. There was also support for negative selection on wing loading in mature male *S. pallipes*, but confidence intervals overlapped zero. Overall, models with wing loading fit the data better than models with PC1.

In **Chapter 2**, I examined the role of body size in mating success in non-territorial male *L. congener* and *L. disjunctus* and territorial male *S. pallipes*. Since *Lestes* males engage in scramble competition for matings and *S. pallipes* males establish and actively defend territories against aggressive conspecifics, I expected body size to play a larger role in mating success in *S. pallipes* than either *Lestes* species. I therefore expected selection on body size to be weak or non-existent in *Lestes* and relatively stronger in *S. pallipes*. Consistent with predictions, there was little or no sexual selection on male *L. congener* or *L. disjunctus*. Also consistent with predictions, large size and wing loading values in male *S. pallipes* conferred a territorial advantage and territorial males had a greater mating success. Large size increased mating probabilities in *S. pallipes* in 1998 but there was correlational selection in 1999 in which small males had a mating advantage early in the season but large males had an advantage late in the season. This phenomenon was attributed to a likely increase in density at oviposition sites late in the season and a concurrent reduction in the cost of death in terms of missed mating opportunities, with the result that male-male competition for matings was greater late in the season than early. Weather was an unpredictable variable that may have affected mating success dynamics through restricting foraging or mating opportunities.

As noted, female and male *Lestes* were smaller in 1998 and female and male *S. pallipes* were larger. This was consistent at both emergence and sexual maturity with the exception of female *S. pallipes* at emergence, but sample sizes were low in this group in 1998. If body size is to be maintained in the long term by selection, then the overall direction of selection should have been positive in *Lestes* in 1998 and negative in *S. pallipes*. Where results indicated selection on overall body size (PC1), they were in the direction opposite to that expected in each case. In male *L. congener* in 1998, there was negative directional natural selection on PC1 over the maturation period and in male *S. pallipes* in 1998 there was positive directional sexual selection on body size. Furthermore, when the three adult selective episodes, immature survival, mature survival and mating success, are simultaneously considered, they do not combine to create overall positive selection in *Lestes* or *S. pallipes*. Selection is therefore unlikely to be responsible for the increase in body size in *Lestes* and decrease in *S. pallipes* between 1998 and 1999. Selection during the larval stage may have been responsible for the change in body size between the years, but this was not measured in this study. Alternatively, weather or another unpredictable environmental variable such as predator or prey levels may have been responsible. In 1999, there was more precipitation, more days with rain and the average temperature over the study period was nearly 2°C lower than in 1998. Conditions such as temperature or predator or prey levels may have caused an increase in the rate of development in larvae with the effect that they emerged at a smaller size, but this hypothesis was not tested.

I found stabilizing selection on body size in only two episodes, both in male *S. pallipes.* In 1999 I found stabilizing selection combined with positive directional selection on wing loading during immature survival and I found stabilizing sexual selection on PC1 in the same year, with alternating directional selection (see above). It is possible that stabilizing selection was only found in this group because it had the greatest number of recaptured individuals, and stabilizing selection is difficult to detect. I found no groups in which natural selection acted in opposing directions between immature and mature survival, although there was negative directional selection on PC1 before maturity in *L. congener* in 1998 and positive directional selection on wing loading after maturity. According to these results, then, we only have evidence to suggest that selection can be responsible for the maintenance of body size in male *S. pallipes* in 1999.

The methodology employed in this study proved to be useful, but some questions proposed in the Introduction remain unanswered. For example, some survival estimates were poor, especially in female *S. pallipes,* and sample sizes were probably too small in some groups to adequately test the possibility of stabilizing selection. A more comprehensive examination of these questions could be achieved by using DNA techniques to measure offspring production in two successive years. This would allow a definitive estimate of the role of body size in mating success and survival over both the larval and adult stages and would concurrently allow an estimate of the heritability of body size in these species.

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